Vol. 18, No. 1 May 1949

THE JOURNAL OF ANIMAL ECOLOGY

COMMONWEALTH INSTITUTE OF ENTOMOLOGY LIBRARY
- 4 OCT 1949
SERIAL Em.431
SEPARATE

EDITED FOR THE

BRITISH ECOLOGICAL SOCIETY

by

CHARLES ELTON

and

DENNIS CHITTY

CAMBRIDGE UNIVERSITY PRESS
CAMBRIDGE, AND BENTLEY HOUSE, LONDON
CANADA AND INDIA: MACMILLAN

Annual subscription: thirty-five shillings (twenty-five shillings to members of the British Ecological Society)

Single numbers: twenty-two shillings and sixpence

World-List abbreviation: J. Anim. Ecol.

THE JOURNAL OF ANIMAL ECOLOGY

Vol. 18, No. 1 May 1949

CONTENTS

PAGE

M. E. Solomon. The natural control of animal populations . . 1

R. J. Goldacre. Surface films on natural bodies of water . . 36

J. S. Colman. The Newfoundland seal fishery and the second World War 40

C. R. Ribbands. The foraging method of individual honey-bees . 47

J. R. Erichsen Jones. An ecological study of the River Rheidol, North Cardiganshire, Wales 67

Sidney C. Hsiao. A limnological study of Erh Hai. 2. Biological features 89

W. S. Bristowe. The distribution of harvestmen (Phalangida) in Great Britain and Ireland, with notes on their names, enemies and food 100

P. A. P. Moran. The statistical analysis of the sunspot and lynx cycles 115

Special Review:

G. C. Varley. Population changes in German forest pests . 117

Reviews 123

Notices of publications on the Animal Ecology of the British Isles . 128

VOLUME 18, No. 1 MAY 1949

THE NATURAL CONTROL OF ANIMAL POPULATIONS

BY M. E. SOLOMON

Department of Scientific and Industrial Research, Pest Infestation Laboratory, Slough, Bucks.

CONTENTS

	PAGE
A. INTRODUCTION	1
B. THEORIES OF CONTROL	3
B1. Early 'biotic' theories	3
B2. The competition theory	3
B3. 'Physical' theories	4
B4. Theories of periodic fluctuation	5
B5. Comprehensive theories	7
C. ESSENTIALS OF NATURAL CONTROL	8
C1. Variation, constancy and control	8
C2. The fundamental relationships in population dynamics	9
C3. Density relationships	10
(*a*) Threshold phenomena	10
(*b*) Density-independent and density-dependent factors	11
(*c*) The form of density relationships	13
(*d*) The causes of density dependence	14
(1) Limited capacity of the environment	14
(2) The significance of competition	15
(3) The density-dependent influence of natural enemies	15
(4) Density dependence and capacity: Conclusions	16
C4. Phases of control	17
(*a*) Limitation	17
(*b*) Suppression	19
(*c*) Conservation	20
(*d*) Release	21
(*e*) Fluctuations inherent in control	21
C5. The level of abundance	22
D. SOME SPECIAL QUESTIONS	23
D1. The relative importance of different factors in control	24
D2. Balance of populations	26
D3. The mode of variation in abundance	27
D4. Do controlling processes cause periodic fluctuations?	28
D5. Reduced variability in complex ecosystems	29
E. SUMMARY	31
F. ACKNOWLEDGEMENTS	32
G. REFERENCES	32

A. INTRODUCTION

While an understanding of the processes which regulate the abundance of animal populations is fundamentally important both to applied biology and to ecology in general, it is a subject on which there are very considerable divergences of opinion. These divergences, which have been so much discussed during the past two or three decades, may be attributed to a number of causes: to the common tendency to embrace partial, one-sided explanations instead of seeking a comprehensive viewpoint; to the diverse views engendered by the study of ecologically different groups of animals, or by a too exclusive attention to either the biotic or the physical aspects of ecology; and, besides these outcomes of specialization, to confusion and misunderstanding over the use of certain terms.

But perhaps the major cleavage is that between the upholders of a primarily deductive and of a primarily inductive approach to the subject. The mathematical theories of population interactions, such as the studies of Lotka, Volterra, or Nicholson & Bailey, have led to various conclusions which are sometimes taken as proven biological facts. These conclusions are the results of deductions from a few simple assumptions. Even when the assumptions are correct as far as they go (and this is not always certain), the conclusions tell us only what would happen in an extremely simple situation immune from the usual environmental disturbances. In relation to natural populations, they should be regarded only as suggestions, though as such they may be an invaluable source of new ideas to be tested in the field.

The important work of Nicholson (1933) resembles the mathematical theories in being primarily deductive in its method. While Nicholson is able to draw on a wide biological knowledge and experience to select and support the premises upon which his theory is founded, and again to relate some of his numerous conclusions to known biological facts, the method remains primarily deductive, and the results cannot be accepted as biological principles until they are shown to correspond with the facts. The views of Smith (1935) resemble Nicholson's in some respects, but the greater part of Smith's argument is

inductive; a summing-up of biological experience rather than a logical construction based on a few facts, principles or assumptions. Thompson's writings on this subject have been of both types, but he gives predominance to the inductive method of theoretical advance. His papers contain many valuable points, and the general outline of a theory which seems essentially sound, yet is scarcely developed beyond the stage of a few preliminary generalizations. In his paper of 1939 there is a critical survey of much of the literature, including a discussion of the methods and status of the deductive theories.

Of course, there is no clear boundary between inductive and deductive theory, and most authors make considerable use of both methods. In so far as the two types are distinct, both are necessary to the development of the subject, and only harm can be done by failure to recognize both the importance and the limitations of the mathematical type of theory. The inductive approach is the one which comes more naturally to students of a subject which is still largely descriptive. There is a great deal to be done in summing up and generalizing ecological knowledge in a form suitable for application in field investigations, so that both aspects of the subject may flourish as they cannot do separately.

The method of this paper is primarily inductive. I have attempted to give a general account and analysis of natural control in the light of the facts available and the theories that have been put forward to account for them. The point is not novelty, nor a complete review of the literature, but an attempt to provide a more complete and coherent theory than has been available, and to clarify certain issues which have been confused. I hope most readers will find something of interest in the result. To make the major ideas plain, I have excluded many minor points; and no doubt have missed many which might have been included. The discussion is developed with reference primarily, though not exclusively, to entomological data and theories. But I believe the principles outlined apply to most types of animal populations and to those of many micro-organisms.

Natural control will be taken to mean that regulation of the numbers of a natural population which keeps them within the limits of a more or less clearly definable though often very wide range of abundance. The simplest and most straightforward view of variations in abundance is that populations tend to increase when conditions are favourable, and to decrease when they are unfavourable. However, it is usual to regard animals as striving (or at least tending) to increase in numbers, but as being kept below certain limits by the resistance of the environment (Chapman, 1928, 1931), by their own limitations and the failure of the environment to satisfy their needs (Thompson, 1929*c*, 1939), by biotic control factors or by physical control factors (various authors), by intra-specific competition and natural enemies (Nicholson, 1933), or by density-dependent factors (Smith, 1935).

Control will be discussed in several different ways corresponding to different levels of organization. The first is the consideration of the *factors* responsible for control, for example, certain animals, plants, or features of the physical environment such as protective niches or temperature. In this approach, the environment, and the population's own activities, are divided into distinct elements which are regarded primarily as acting separately upon the population, though interdependent action is not necessarily ignored. Secondly, a better integrated approach is the consideration of working relationships or *processes* such as competition, parasitism, and density dependence. Thirdly, instead of analysing control in terms of factors or processes we shall sometimes consider it as a complete phenomenon, and this of course involves the consideration of *population variations* (this term will always be used in the sense of numerical or density variation only). Finally, control will also be considered as a part of the complex web of relationships which is a feature of the ecological entity comprising the population and its total biotic and physical environment (the *ecosystem*, to use the term suggested by Tansley, 1935).

It will be seen that the paper is divided into primary sections, A, B, etc., some of these being divided into secondary sections such as B1, B2, etc. In each secondary section the discussion is confined predominantly to one or other of the above-mentioned levels.

The plan of the paper may be summarized as follows: In section B a brief review of theories of control is given, progressing somewhat irregularly from factor theories to those with a more comprehensive approach. Section C is an attempt to outline a theory of control which is a synthesis and development of certain familiar generalizations; for convenience of presentation, the order of the secondary sections does not follow the series of organizational levels—C1, C4 and C5 deal with population variations, while C2 considers the whole ecosystem, and C3 is an analysis chiefly on the level of processes. Section D deals with certain points, some of them less well established, which are placed here in order to leave the main section C clear of too many secondary issues. The trend in this section is from analysis by factors (D1) to the level of population variations (D2–D4) and thence to the most comprehensive viewpoint (D5).

For the purposes of analysis and discussion, certain terms are newly defined or given a more precise meaning than usual. While I have tried to avoid misleading usages, it may assist readers to have the

following reference list, showing the pages where the terms are defined or explained. Those not in inverted commas are employed in a sense well established in the literature. Terms used in one place only are not included in the list.

	PAGE
balance	26
biocoen	10
'capacity'	14
carrying capacity	5
(inter-)compensation	19
competition	15
'concurrent'*	13
'conservation'	20
density-dependent	4, 11
density-independent	4, 11
'density relationships'	13
ecosystem	2, 10
equilibrium	26
factor	2
'favourable'	11
'functional'*	16
'inverse'*	13
'limitation'	17
'numerical'*	16
overpopulation	5
'performance'	14
'release'	21
'restricted variation'	9
'supply factors'	12
'suppression'	19
'threshold phenomena'	10, 11
undercrowding	11
'unfavourable'	11
'variation(s)'	2

* Types of density relationships.

The term *population* as used here means a number of organisms of the same species forming a more or less frequently interconnected group, separated more or less clearly from other groups of the species.

B. THEORIES OF CONTROL

In this section, the theories of control that are of most interest at the present day are briefly reviewed. Comments on many important points are postponed to later sections, though some are taken up directly here. The selection, classification and the relative prominence given to the various theories have inevitably been somewhat arbitrary, and in this matter I must ask the indulgence of readers and authors.

A fuller discussion of the theories of the German biologists mentioned has been published by Schwerdtfeger (1941), and Thompson (1939) has discussed the theories put forward by British, French and American entomologists.

Among the theories of control, there is an historical trend from earlier theories which sought to explain control upon a comparatively narrow basis, to later theories which are more comprehensive. There is a very general tendency among the earlier (and some more recent) theories to emphasize the importance of the physical environment in control, while underestimating the importance of the biotic factors, or vice versa.

B1. Early 'biotic' theories

Of the two viewpoints mentioned above, the one more in keeping with the Darwinian trend of biology was that of the predominant importance of the biotic factors. Escherich (1914, 1924), for example, held that control of insect populations is due primarily to natural enemies, especially parasites, and that outbreaks are due to an unbalance brought about by the effects of weather conditions or food supply upon the host or its enemies (cf. Howard & Fiske, 1911).

Others, such as Friederichs (1927), recognized the complexity of the relationships between a population and its biotic environment. Control was attributed primarily, not to parasites only, but to the whole 'biocoenotic complex'.

B2. The competition theory

The work of Nicholson (1933) is related to the earlier parasite theories, inasmuch as it is predominantly a biotic theory of control. Nicholson's paper comprises (*a*) a general theory of control, and (*b*) a theory of the interactions between populations of enemies and those of their hosts or prey, and a study of the oscillations which are deduced to arise from these interactions. Confining our attention to (*a*) we may refer to the relevant parts of Nicholson's summary (p. 176):

'The densities of animal populations are known to bear a relation to the environmental conditions to which they are subject, and the existence of this relation shows that populations must be in a state of balance with their environments. For balance, it is essential that the action of a controlling factor should be governed by the density of the population controlled, and competition seems to be the only factor that can be governed in this way. Examination of the competition to which animals are subject shows that it is generally competition between animals when seeking the things they require for existence, or competition between natural enemies that hunt for them.

'Detailed investigation of the question of competition between searching animals shows that, whether the animals are controlled by competition for food, or for suitable places in which to live, or by the competition of their natural enemies, there is for each species a particular density, referred to as the "steady density", at which balance exists. The value of this steady density depends upon the properties of the species, the properties of the species with which it

interacts, the nature of this interaction, and the properties of the environment.

'Competition always *tends* to cause animals to reach, and to maintain, their steady densities. Factors, such as climate and most kinds of animal behaviour, whose action is uninfluenced by the densities of animals, cannot themselves determine population densities, but they may have an important influence on the values at which competition maintains these densities.'

Various points mentioned in Nicholson's paper suggest the outlines of a broader view, obscured, however, by the too exclusive emphasis on biotic relationships. Thus it is noted that competition is the result of environmental limitations, though most emphasis is placed on the competition and very little on the environment. The modifying effects of climate and other factors on the results of competition are recognized. It is mentioned that competition may force surplus animals into unsuitable parts of the environment, where they are destroyed by the physical factors (pp. 139, 173; cf. Thompson, 1929*c*).

These points were given much stronger emphasis by Smith (1935) in his theory of the control of insect populations. While this had certain affinities with the competition theory, there were some important differences from Nicholson. Smith emphasized the distinction which had already been discerned by Howard & Fiske (1911) and Thompson (1928) between *density-dependent* mortality factors, which destroy a percentage that increases as the density increases, and *density-independent* mortality factors, whose effect is not related to population density. He considered the density-independent factors to be mainly climatic, while density-dependent factors included natural enemies, disease organisms, and also the supply of food, space, protective niches, etc., when these are limited, 'since they cause competition'. In spite of this last clause, he laid as much emphasis on density-dependent factors as agents of control as he did on competition. He allowed an important role to various processes which Nicholson had regarded as only minor items in control. He not only extended the category of density-dependent factors to include the aspect of the physical environment mentioned above, but also recognized that climate 'often operates quantitatively in much the same way that is characteristic of biotic factors, that is, it destroys a percentage which increases with density....It seems most probable that this takes place through the existence of protective niches in the environment which are more or less limited in number. Individuals in excess of this number and which can not therefore attain these niches are destroyed by unfavourable climate....' (Pp. 894–5.)

In short, Smith's paper provides a link between Nicholson's theory and the more comprehensive theories of control, which are discussed in the last part of this section.

B3. 'Physical' theories

The vigorous development from the 1920's onwards of experimental work showing the importance of the influence of temperature and humidity on the rates of development, reproduction, etc., of insects, was naturally reflected in new theories of control. Thus Bodenheimer (1928, 1930, 1931) held that the population density of insects is regulated primarily by the effects of weather conditions on their development and more particularly on their survival. He held that a mortality of 85–90% among the early stages is the rule, and that the later reduction of the survivors by enemies, however striking to the observer, is therefore of minor importance. Janisch (1938, 1939) attributed basic importance rather to the influence of non-optimal weather conditions on the general 'constitution' of the organism, affecting its general performance and vigour. Uvarov (1931), emphasizing the strong influence of climatic conditions upon the rate of development and survival of insects, and the obvious correlation between population fluctuations and changes in the weather, seems to have regarded climatic factors as the major controlling agents. In a more recent attempt to sum up the position, Bodenheimer (1938) concluded that 'under normal conditions climate really controls population density in being responsible for the highest degree of destruction. It is, as a rule, the main factor as long as the saturation point of environmental capacity has not yet been approached. This is the normal condition for most animals and even for the longer span of life of species which are inclined to outbreaks.' On the other hand, he adds, biotic factors are important chiefly when a population has approached the environmental capacity, for only density-dependent factors can be relied on to reduce the numbers; but the special stress laid on parasites was unjustified.

These concessions made by Bodenheimer were scarcely such as to satisfy many of the critics of his theories. Schwerdtfeger (1941) points out that while they stimulated many useful new lines of investigation, the weather theories are fundamentally unsound. There is ample evidence that the high rate of mortality due directly to weather conditions, as claimed by Bodenheimer, is not at all general. But the fundamental weakness of these theories, in Schwerdtfeger's view, is the failure to grasp the close and many-sided dependence of a population upon the biocoenotic complex. The most damaging criticism, however, is that made by Nicholson (1933), that these theories fail to explain how physical factors, however important as causes of *variation*, could possibly *regulate* populations.

B4. THEORIES OF PERIODIC FLUCTUATION

(*a*) *Overpopulation theories*

Certain theories intended primarily to explain periodic fluctuations in numbers have an important bearing on natural control. A number of these are based on the general idea that some populations in favourable environments are able to increase in density over a period of years until a level is reached at which 'overpopulation phenomena' develop; these phenomena appear more or less suddenly and reduce the population to a low level. They then relax or disappear and the population goes through another period of increase. These theories relate to particular types of animals and differ as regards the overpopulation phenomena which are supposed to be effective.

(1) Eidmann (1931, 1934), reported that certain forest insects in Germany, in favourable areas, exhibit a gradual increase followed by a rapid fall in numbers, every 10–12 years. He concluded that the decline is due to 'overpopulation phenomena', such as overcrowding, damage to the environment, reduced fecundity, increased susceptibility to diseases, food shortage, and the increase of enemies (Eidmann, 1937). Schwerdtfeger (1941) showed that relatively few populations of the insects concerned show regular fluctuations, and that the reversal of increase (in one species and place) tends to occur at very different levels, often far below the density usually associated with the idea of overcrowding. He concluded that this theory can apply only in a very limited way, and that its chief value is in drawing attention to the importance of overpopulation phenomena as an item in a larger complex of controlling processes.

(2) Dymond (1947) put forward a theory to explain the periodic fluctuations of certain mammals and birds in Canada. In Dymond's words: 'Briefly the theory here offered to account for the periodicity in the fluctuations of the populations of lemmings, hares, voles, grouse, etc., is that the biotic potential of these animals is definitely greater than the normal resistance of the environment in which they live. In other words they are endowed with too high a reproductive capacity and it is the monotony or relative uniformity of the Arctic and far northern environment that accounts for the regularity with which they increase to the unstable level of numbers which brings about the periodic decline.' As to the causes of the decline: 'In the case of dense populations there appears to be a race between disease, emigration and starvation as to which is to reduce the numbers, with the decision determined largely by the reaction of the species to crowding.'

(3) Another type of idea, which may be referred to the general category of overpopulation theories, looks to predators as the chief agents of control, but sees them as becoming really effective only when the 'carrying capacity of cover' in the environment has been exceeded. For a clear account of these ideas, put forward by Kalabukhov (1935) and others, we may quote from Elton (1942, p. 87): 'Kalabukhov points out that as a population of voles or mice or ground squirrels increases, the food supply on the occupied areas will tend to diminish. When food is scarcer the animals move about over larger distances. This greater movement exposes them more to their enemies and so mortality through these predators will be greater. Also, the deaths from accidents may be more frequent. "The more food there is in a given territory, the smaller is the radius of movement of rodents, and the less the possibility of their death from predators"... . We might add to this (though he does not) the analogous and parallel action of disease: favourable food supply encouraging resistance, reduction of food supply, increased movement promoting the spread of disease organisms with a resulting higher (sometimes catastrophic) mortality.

'Kalabukhov's theory has in it a flavour of the American idea of the "carrying capacity of cover", widely current now in game-bird population studies. This was crystallized in American research upon the bobwhite quail, which claims that there is a sudden rise in destruction by predators among quail populations that have begun to overflow the normal protective cover. Kalabukhov does not seem to have considered the fact that the food supply of many mouse-like rodents, and especially voles, *is* their cover, and that eating down the available food, besides causing increased movements, may often automatically expose the animals more to their enemies. This further concept reinforces his own theory.'

While the efficacy of predators as controllers of mammalian and bird populations is very doubtful (Elton, 1942; Errington, 1946), there is no doubt that the 'carrying capacity' or 'threshold of security' relationship is an important element in natural control.

(4) Clarke (1936) attributed the periodic (9–10-year) diminution in numbers of the ruffed grouse in Ontario to disease, caused by a blood protozoan or some other agent, which attacked the young birds at high population density.

In the same area, MacLulich (1937) studied the varying hare, which has a 10-year cycle, and concluded that the crashes of this species are chiefly due to various diseases. But the work of Green and his collaborators, chiefly in Minnesota, seems to establish that the only important cause of the periodic decline is 'shock disease', an idopathic hypoglycaemia which brings about a progressive increase in mortality of the young hares (Green, Larson & Bell, 1939; Green & Evans, 1940).

MacLulich observed: 'Population figures for the northern part of Frontenac county showed that in

times of abundance the hares occupied practically all types of habitat, whereas in times of scarcity they were confined to their favourite habitat.' Concerning the ruffed grouse, Clarke reported: 'The most suitable territories in any given area are occupied every year, less suitable ones only when pressure of increasing populations makes this necessary.'

(5) Besides the concept of overpopulation, most of these theories use this associated idea of 'overflow' from favourable spots into less favourable parts of the environment as the population density increases. The same idea was used by Thompson (1929*c*, 1939) in his theory of the control of insect populations. It was mentioned by Nicholson (1933) in relation to competition, and Smith (1935) noted its significance in enabling climatic factors to operate in a density-dependent manner.

This and other aspects of environmental capacity will be discussed in a later section. The chief point of interest at this stage is that, owing to the heterogeneity of most environments, overpopulation phenomena tend to set in long before the whole area is 'saturated'.

(6) In general, there is no reason why overpopulation phenomena should be regarded as peculiar to populations which fluctuate periodically. In fact, they are known to be widespread and common. But whereas they may possibly supply a complete explanation of the control of certain populations which fluctuate regularly, in general they do not account for the whole process of control. For example, in some cases it is quite clear that predators or parasites successfully control a population at a relatively low level, far below what could reasonably be called overpopulation. As will be seen in later sections, overpopulation phenomena are only one item of a larger category of processes which can contribute to natural control.

(*b*) *Enemy-prey oscillations*

The overpopulation theories deal with fluctuations as characteristics of primary, plant-eating animal populations; fluctuations of their predators are regarded as by-products, or reflexions of the primary ones. Another type of theory places equal emphasis on the fluctuations of a population and that of its predator (or parasite), and in fact regards the fluctuation as a result of the interaction of the two populations. This is the mathematically evolved theory, of which variants have been produced by Lotka (1925), Volterra (1926, 1931, etc.), and Nicholson & Bailey (1935) (see also Nicholson, 1933). Assuming a constant physical environment, and an enemy-prey interaction characterized by a very simple behaviour pattern and not interfered with by other species, it is calculated that the two populations should oscillate regularly above and below a mean level of density. The graph of density against time is in the form of the now familiar wave-like curves, that of the enemy following somewhat later than that of the prey. The precision of these mathematical demonstrations, and the elegant regularity of the results, are achieved by assuming a very simple and regular (or constant) set of conditions, such as we should seldom expect to find in nature. These theories have not the same status as those based more directly on natural phenomena. While they are certainly a source of valuable new suggestions and working hypotheses, their conclusions, as remarked at the outset, cannot be regarded as biological generalizations unless they are proved by observation or experiment under natural or near-natural conditions. A valuable preliminary is to test them in laboratory experiments.

It is a significant fact that, even under highly simplified conditions in the laboratory, the periodic oscillations predicted by the mathematical theories can be demonstrated only with great difficulty. Gause (1934) produced the phenomenon in mixed cultures of *Paramecium* and yeast, but only by careful manipulation of the cultures. He also demonstrated it with *Didinium* and *Paramecium* together, but again only by repeatedly introducing additional individuals of both species. De Bach & Smith (1941) were able to bring about the greater part of a complete cycle with interacting populations of housefly pupae and the parasite *Mormoniella*. There were seven successive 'generations', which were in fact separate 24 hr. experiments under the same conditions except that each experiment after the first was started with a number of parasites equal to the number of puparia parasitized in the previous experiment, and with a number of puparia equal to twice the number escaping parasitization in the previous experiment.

While recognizing the great interest of these experiments and their results, we may note that they seem more akin to the hypothetical situations of the theories than to natural conditions. A wide gap remains to be covered.

It seems probable that the periodic fluctuations of *Tribolium* in cultures are of the same nature as those we have been discussing, but they must be very complicated, for the larvae and adults act as predators upon the eggs, and the larvae are parasitized by the Sporozoan *Adelina* (Chapman, 1928, 1933; Chapman & Whang, 1934; Ford, 1937; Park, Gregg & Luterman, 1941; Park, 1948).

Since periodic oscillation is difficult to produce even under rigidly controlled experimental conditions, it is doubtful whether many oscillations observed in nature can correctly be claimed as examples of it. Any such tendency is likely to be complicated and obscured by the effects of many factors not considered in the theories.

It might be expected that examples of these 'classical' predator-prey oscillations could be found

among the populations of rodents and their predators, discussed by Elton (1942), Dymond (1947) and others. It seems to be generally agreed, however, that the predators 'are seldom a master factor in bringing rodent outbreaks under control' (Elton, 1942, p. 60; see also Errington, 1946). Only if a predator population, whose fluctuations followed those of the prey, also played a dominant role in the reduction of the prey at the periodic crises, should we have good reason to suspect the presence of a relationship like that described in the mathematical theories. If, as held by Dymond, the Arctic environment is steady enough (or barren enough, to mention another possibility) to allow the appearance of regular fluctuations due to overpopulation phenomena, it is reasonable to seek there, if anywhere, for examples of periodicities controlled by predator-prey interaction.

(*c*) *The meteorological theory*

Elton (1942) has examined a very extensive body of data on rodent populations, and concluded that periodic changes in the physical environment must play some part in causing the fluctuations in numbers, or at least in making them regular (cf. Huntington, 1931; Severtzoff, 1934; Errington, 1945). But however important physical periodicities (seasonal or otherwise) may be in relation to fluctuations of populations, they do not seem to offer an explanation of natural control. The main interest of these phenomena to the present discussion lies in the question, to what extent they account for the periodic population fluctuations which the overpopulation theories were evoked to explain. But even in this respect they are not of great importance here, for the significance of overpopulation phenomena as agents in natural control by no means depends only on the importance or otherwise of these phenomena as causes of periodic fluctuations.

B5. COMPREHENSIVE THEORIES

The term comprehensive is intended here to apply to theories which do not attribute control predominantly to parasites, competition, or biotic factors, nor on the other hand to physical factors, but rather recognize that all types of factors may be involved, and that relationships which are predominant in some circumstances may be relatively insignificant in others. The case for such a standpoint will be more fully examined later. The theories that are most in keeping with such a broad view (at least in the entomological field) are those of Thompson (1929*c*, 1939) and Schwerdtfeger (1941).

Thompson's viewpoint may be summarized as follows: Each species has its own characteristics, including specific needs and limitations. Optimal environmental conditions, in which these needs are (best) satisfied, are approached at relatively few points. The species multiplies in these favourable places, and the surplus animals so produced are forced out into less favourable places, and so on, so that the increase of the population is first retarded and finally stopped. In general, the control thus exercised is due not only to one or two 'controlling factors' which predominate at all times and places, but to the whole complex of environmental factors, biotic and physical, of which different factors are predominant in different situations. Density effects also operate against increase in the favourable situations. Furthermore, the environmental conditions are subject to change and so bring about reductions in density from time to time. Control is generally due mainly to physical factors in the environments less favourable to life, where density is low; biotic factors are important chiefly in physically favourable environments where density is high. The diversity and other characteristics of the physical environment are an essential element in competition and other density-dependent processes.

Thompson does not attempt any pronouncement as to the relative importance of physical and biotic factors to control *in general*, but contents himself with the conclusion that control is due to the whole complex of factors of all types, of which some are predominant in some circumstances, others in others. The idea of 'overflow' from favourable niches was given prominence by Thompson (1929*c*), and also by Smith (1935), though Nicholson (1933) did not attach special importance to it. The occurrence of this idea in the overpopulation theories has already been noted.

Schwerdtfeger (1941) deals primarily with population variations and their causes rather than with control. He considers in some detail the effects of various factors upon the egg-output and the mortality of insects. His data on forest insects support the conclusion that a large number of factors of all types operate together and in succession, with varying intensity, to bring about the major fluctuations in numbers. The importance of particular factors varies with the species, stage of development, density, time and place.

On the question of control, he accepts, without discussion, the conclusion of Smith (1935) and others regarding the role of density-dependent factors as the regulators of numbers. But he has also another viewpoint on this matter which arises from the consideration of the whole ecological system of which the particular population is a part.

The many factors of significance to the variation of a population he regards as an entity, the *gradocoen*, which is an intricate system comparable to a three-dimensional network (cf. the concept of the *holocoen* put forward by Friederichs, 1930). It includes the population itself. This system tends to achieve and

maintain an internal equilibrium; systems which fail to maintain equilibrium break up and are absorbed by others, or replaced by newly reconstituted systems. Any undue deviation from normal by one of its constituents is opposed by the elasticity and stability of the system. This idea will be examined below.

Meanwhile, we may note that Schwerdtfeger and Thompson agree that in the problem of control we have to do with a complex of factors, not one or a few 'controlling factors'. Schwerdtfeger goes further than Thompson in considering the complex as a system, operating as an entity, and tending to preserve an internal equilibrium. According to Schwerdtfeger, control is due to this equilibrating tendency of the whole system of which the population is a part, but at the same time he accepts the idea that the actual regulators within this system are the density-dependent factors. According to Thompson, the density-dependent processes which bring about control arise from the complex of factors, including both biotic and abiotic types.

Schwerdtfeger's 'gradocoen' is a sort of ecological unit, comprising all the biotic and abiotic elements directly or indirectly of importance to the variation of the population selected for study. It consists of a 'holocoen' (Friederichs, 1930) or 'ecosystem' (Tansley, 1935), except that we exclude any elements which seem to be irrelevant for our purpose.

According to Schwerdtfeger, such a system would maintain an internal equilibrium; but as is often the case in biology, the word is used rather loosely here. It is not meant to imply that the population and all the relevant environmental factors are constant, but it means that they are dynamically interrelated in such a way that excessive variation by any of them is checked by other components in the system, or, more correctly, by the elastic inertia and stability of the system as a whole.

Whether or not it is advisable to use the term equilibrium in this way, for our purpose the chief points in this part of Schwerdtfeger's theory are the ideas involved in his view of the interconnectedness and elastic stability of the gradocoen. These will be discussed in the sections immediately following. Of course, the idea that all types of factors form an interdependent system has been approached or adopted by a number of ecologists in works not primarily concerned with control, e.g. Allee (1934*a*), Eggleton (1939), and Park (1942).

C. ESSENTIALS OF NATURAL CONTROL

C 1. Variation, constancy and control

The causes of variations in numbers are often obvious enough in a broad way, though precise knowledge has been reached only for a few ecological situations. It is widely agreed that variations in the physical environment are, directly or indirectly, the major cause of population variations. That is not to say that biotic factors, such as food supply and enemies, do not generally play an important part in bringing about variations; nor that, when the physical environment is relatively constant, they do not come to play the dominant role. But in the great majority of cases, and particularly with insects, it is clear enough that numerical variations primarily reflect changes in the weather. The weather affects populations in many different ways; it can influence the reproductive rate and the mortality rate, the food supply, and the activity of enemies, to say nothing of more indirect and complex relationships. Even variations which seem to be due primarily to a succession of separate generations, as in many insects, may largely reflect favourable and unfavourable periods in the seasonal cycle; and in any case, seasonal climatic factors are responsible for the sorting out of the generations and keeping them separate, for example by killing off all but one particular resistant stage at regular intervals. To discover which aspects of weather are significant in causing variations in numbers, and precisely how they do this, often requires very close knowledge of the habits and habitats of the species concerned.

The range of fluctuation from year to year is very variable. The ratio of the highest to the lowest annual population observed was 32 : 1 for a population of the coccid scale insect *Ceroplastes floridanus* in Palestine, but only 3·8 : 1 for the scale *Parlatoria camelliae* (Bodenheimer, 1938, p. 103), over 33 : 1 for annual larval populations of wheat midges at Rothamsted (Barnes, see Williams, 1947), over 10,000 : 1 for the pupae of the moth *Panolis piniperda* in certain localities in Germany (Schwerdtfeger, 1941, p. 266), and 36 : 1 and 24 : 1 for the Canadian sockeye salmon in two different rivers (Dymond, 1947). By marking and retrapping, Green & Evans (1940) estimated the population of the varying hare on an area in Minnesota; the rates of the highest to the lowest annual population in the cycle of the 1930's was about 10 : 1. Schwerdtfeger (1935) gave data on the variation from year to year in the population density of four species of forest insects in various places in Germany, over the period 1885–1932. The greatest increases recorded are 29-, 41-, 47- and 93-fold respectively; the greatest decreases are 125-, 200-, 250- and over 3000-fold respectively.

The range of fluctuation in numbers within a year is again very variable, even for the same population. Bodenheimer's data from monthly counts of *Ceroplastes* show the ratio of the highest to the lowest monthly count in 1929 was 270 : 1; in 1931 it was only 7 : 1; for *Parlatoria* it was 43 : 1 in 1936, but only 9 : 1 in 1933. Cutler, Crump & Sandon (1922) reported

that the numbers of a species of Protozoa in the soil sometimes varied from a few hundred to 400,000 or more within 24 hr.

Some populations give an impression of steadiness rather than of variability in numbers. None, of course, are perfectly constant, and some degree of variation is always found upon close examination. When a fairly steady level is maintained, it seems generally to be due to self-regulatory action by the population itself in a comparatively stable environment. For example, some of the birds which maintain a territory system tend to occur in the same numbers year after year in the same locality (Nice, 1937; Lack, 1943). Complete annual censuses of the heron population of Cheshire and South Lancashire in 1939–45 gave figures ranging from 68 to 108% of the 'normal' population total; and this was during a period of relatively 'marked fluctuations' (Alexander, 1946). Populations of *Drosophila*, cultured under constant physical conditions on an adequate food supply, have been reported to rise to a more or less stationary level of abundance (Pearl & Parker, 1922*a*, *b*). The data of Bodenheimer (1938), however, show marked oscillations within a limited range of high numbers, and he described this phase of the population's existence as the 'period of oscillations about a stable maximum'. A nearly steady maximum abundance under special culture conditions has also been observed with *Tribolium* (Chapman, 1928), but over long periods the numbers of this beetle pass through marked oscillations (cf. Chapman, 1933; Chapman & Whang, 1934; Ford, 1937; Park *et al.* 1941). This may be attributable mainly to cannibalism by the larvae and adults, and to the Sporozoan *Adelina*, features which are to some extent special, but by no means unique. It appears that certain other beetles, cultured under similarly standardized conditions, also suffer persistent fluctuations in numbers (Park *et al.* 1941; the coefficients of variability were 39% for *Tribolium*, 35% for *Gnathocerus cornutus*, and 69% for *Trogoderma versicolor*. See also Crombie, 1945, 1946). In other words, the 'equilibrium' number is steady only in a loose sense, and a close approximation to absolute steadiness is very difficult to maintain, even under artificial conditions.

It may be that a closer approach to a steady number can be achieved by some animals, but, owing to experimental difficulties and the long time involved, population growth experiments are often abandoned soon after the numbers appear to have reached a maximum. As shown by the above-mentioned experiments with beetles, the apparent constancy may be only a temporary phase, followed by a succession of fluctuations which may be relatively slow. Whatever happens in laboratory cultures, it is obvious that in nature, climatic variations, to say nothing of other important factors, are likely to upset any tendency towards precise constancy.

Whether we emphasize the steadiness or the variability of populations is largely a matter of our scale of reference. In spite of variations in density, it is very often possible to recognize for a population a characteristic general level or range of density. Some species, in certain environments, usually occur in large numbers, while others usually occur sparsely. This characteristic order of abundance may be quite different for the same species in different environments, and it may change from time to time even for the same population. Nevertheless, it can generally be specified for a given population over a more or less extended period. It may be regarded as an index of the capacity of the environment to support the species concerned, and of the species to maintain high numbers in that environment.

In discussing the variability of populations, Smith (1939; and cf. Chapman, 1931, p. 204) wrote: 'Paradoxically, animal populations are characterized both by their stability and by their incessant change. Some biologists emphasize one of these aspects, some the other. Actually these expressions are both descriptive of animal populations just as much as they are descriptive of the weather, which changes from day to day but which over a longer period of time is very stable. These characterizations of populations are not inconsistent if it is remembered that they are meant in the relative sense only. Population densities therefore have both static and dynamic qualities, the distinction being analogous to that between climate and weather.'

Undoubtedly there are elements both of constancy and of variability. In a precise sense, populations often vary greatly in numbers; in a very broad sense, they may be regarded as fairly constant. But since an alternation between two opposite viewpoints is often inconvenient or confusing, it seems preferable to combine them and to think of populations as undergoing *restricted variation*. This is the state to which populations are confined by the processes of natural control. If there were no control, variation would be unrestricted.

C2. The fundamental relationships in population dynamics

To understand the variations in numbers within populations, and the restriction of these variations, we must consider first of all the most general relationships between a population and its surroundings. The total situation comprising a population in its biotic and physical environment is divisible into many components, among which there are many interrelationships of varying significance. Everyone is familiar

with the complexities that appear if we set down a number of components, and draw in the various influences which are known to operate, whether in general or in relation to an actual example. We soon reach an impressive tangle of interrelationships, and the conclusion becomes inescapable, that the population and its whole environment operates as a single complex.

Nevertheless, we can reach more precise knowledge of the processes at work only if we deal with one or a few aspects of this complex at a time, and consider them almost in isolation. There is a natural tendency to forget the complex background from which the objects of study have been abstracted. This gives rise to many optimistic but wrong conclusions. All conclusions drawn from simplified pictures or experiments should be referred back to the natural situation, to find to what extent they remain valid, or can be expected to do so, in the complex conditions which prevail there.

The most realistic view, though not invariably the most useful, is one which embraces the whole complex of population and environment. Tansley (1935) introduced the term *ecosystem* for the system comprising the animals and plants in a given environment, and the physical environment itself. The term *holocoen* seems to have the same meaning (Friederichs, 1930; Schwerdtfeger, 1941) and the idea of an all-inclusive 'super-organismic unity' was discussed by Allee (1934*a*).

Clements & Shelford (1939) set out to classify the interactions within such a system. They considered the primary set of interactions to be that between physical environment and the entity comprising all the inhabitant plants and animals. This totality of organisms has been called the *biocoen* (Friederichs) or *biome* (Clements). Such a procedure implies, among other things, that the plants and animals are influenced by the physical environment in analogous ways. It seems a very reasonable viewpoint, and in fact the idea of the biome as an entity has gained wide acceptance (Tansley, 1935). (The use of the alternative terms *biotic community* and *complex organism*, and the viewpoints implied, are much more controversial steps, but need not concern us here. It must be noted, however, that the term biome has also been used by some writers to denote a biotic community, or a biotic formation, e.g. Carpenter, 1939.)

In whatever manner we may find it convenient to subdivide the ecosystem, one of the most difficult and least realistic of major divisions is, in some ways, that between a population and its environment. But because such an approach is demanded by long-established traditions of thought, and because it is so familiar, we tend to overlook the serious difficulties it raises.

A major anomaly appears in relation to endoparasites and other organisms living inside the bodies of animals. If we attempt to make any simple descriptive distinction between the host population and its environment, we are confronted with the question: Are intracellular symbionts, trypanosomes in the blood stream, toxins released by parasites into the blood, etc., to be classed as parts of the host, or of the environment? Any simple spatial distinction between the two is impossible, and any more complicated distinction is very difficult to maintain consistently.

Another serious anomaly arises if we try to think in terms of the population as something tending to increase, and of the environment as something which opposes this increase. This distinction between a striving population and a resistant environment cannot easily be maintained because a part of the restrictive processes (sometimes a major part) arises from activities of the population itself, such as cannibalism, intra-specific competition, spoiling of the environment, etc. In fact, the tendency to increase may be opposed as much by the activities of the population itself as by the environment, though for the most part we are faced with an intricately combined action by population and environment together. Hence any idea that the environment can be clearly distinguished from the population on a functional basis is illusory.

The reason why the population/environment distinction gives rise to such anomalies is that *the population functions in relation to a whole which includes itself*. It is therefore better to think of the population as an integral part of the ecosystem. If we wish to consider the population as an entity in relation to its ecological setting, that setting should be the ecosystem, rather than an imaginary 'ecosystem minus the population', called the environment. This is not to say that the environment concept should not be used, but rather that we should remember its defects and be ready to replace it whenever necessary.

C3. Density relationships

(*a*) *Threshold phenomena*

As we have noted, the density or numerical status of a population is usually variable, but only within certain limits. The essential feature is that, as density increases, the probability that the trend will be reversed, that the numbers will begin to suffer a decline, becomes greater and greater, until we reach an uppermost level beyond which the population density is never observed to pass. Correspondingly, the proportional rate of increase often declines as population density increases (cf. Allee, 1931, 1934*b*; Pearl, 1926; and others); such a relationship is of course the basis of the logistic curve and formula for population growth.

These relationships come about in two ways: (*a*) through the fact that new and more severely

unfavourable processes come into play at successively higher levels of density, and (*b*) by an increase in the intensity of action of various individual factors or processes (density-dependent action).

The entry of new types of unfavourable* processes as density increases was pointed out by Howard & Fiske (1911), who concluded, from their work on leaf-eating Lepidoptera, that parasites were the predominant unfavourable factor at moderate densities, disease when the insects had reached a density far beyond the average level, and famine at the very highest levels. MacLagan & Dunn (1935) concluded that natural populations are automatically checked by density effects (such as depression of reproduction by overcrowding) when all the other inhibiting factors have failed. Some of the well-known phenomena of overcrowding, which will be referred to later, appear only above a certain high level of density, though others are merely intensifications of activities which occur at all densities.

On the other hand, certain 'undercrowding' phenomena, such as a reduced reproductive rate because of infrequent encounters between the sexes, occur only *below* a certain level of density. On the whole, this class of unfavourable influence is much less important than the reverse.

Little is known about thresholds of activity for favourable processes, but the truth and importance of the threshold principle in relation to unfavourable influences is obvious enough. A great deal remains to be done, of course, in demonstrating how it works in specific cases, determining the threshold levels, and studying the causes of variation in these levels. The quantitative data now available relate chiefly to the densities at which crowding effects begin to hinder the increase of certain species. Some interesting figures published by Errington (1945) on the rates of increase and of decrease of bobwhite quail populations in relation to density show very clear threshold effects.

(*b*) *Density-independent and density-dependent factors*

The distinction between mortality factors whose intensity of action (proportional effect) depends upon the population density, and factors whose action is independent of density, was first drawn by Howard & Fiske (1911), and later by Thompson (1928), Zwölfer (1930), Smith (1935) and others. We shall make this distinction not only among mortality factors, but among all types of factors or processes.

There has been (and still is) a general tendency to identify density-dependent action with biotic factors, and density-independent action with physical factors, although Thompson (1939) pointed out that nature is by no means so simple; the extent to which such a classification over-simplifies and distorts the facts will be apparent from the following discussion.

To consider, first, the *density-independent factors*, we may quote from the valuable paper by Smith (1935, p. 890): 'In general, excessive heat or cold, dryness or humidity, wind or rain will destroy the same percentage of insects regardless of whether they are abundant or rare. Intrinsic weaknesses . . . also belong in this category, as would non-contagious or non-infectious diseases, and malnutrition due to *condition*, but not *quantity*, of food.' (The 'intrinsic weaknesses' concerned are postulated as the causes of the high mortality regularly observed among certain insect larvae.) Density-independent factors often vary a great deal in their intensity from time to time, but these variations are independent of the population density, even if there is sometimes an accidental parallelism.

Notwithstanding the above quotation, Smith himself (loc. cit.) and Thompson (1929*c*, 1930, 1939) pointed out that climatic and other physical factors are by no means necessarily density-independent in their effects upon the population. This is because they often operate in combination with density-dependent processes. For example, in the event of drought (density-independent), members of a susceptible species may congregate in niches where extra moisture or protection from evaporation enables them to survive. But the proportion able to survive depends on the size of the population. The favourable space may be sufficient for no more than x individuals. Then roughly x individuals will survive whether the original population was $100x$ or $1000x$. This is a picture, though admittedly an over-simplified one, of density-dependent action brought about by the limitations of the environment (Thompson), or by competition (Nicholson, 1933), according to one's viewpoint. For the present purpose, it shows how a 'density-independent factor' may be involved as an essential element in a density-dependent process; for there would have been no such all-important competition or selection by these niches without the drought conditions in the rest of the environment (cf. Thompson, 1939). This is the sort of complication to be expected from the fact that different factors do not act in isolation, but are subject to the dynamics of the whole ecosystem.

The example also emphasizes the point that it is sounder to consider density-dependent or density-independent processes or actions, than to classify factors on this basis. Not that the latter is impossible. Even in the above example, we may say that the physical factors contribute a density-independent component to the total operation.

Another way in which density-independent and density-dependent factors may be involved in

* That is, unfavourable to increase or to the maintenance of the present density. 'Favourable' will be used in the opposite sense.

combined action is seen in cases when weather conditions promote the outbreak of disease. Thus according to Eckstein (1939), certain outbreaks of bacterial or fungal disease among cockchafers in Germany are primarily due to the effects of climatic conditions upon the susceptibility of the larvae and the properties of the soil, as well as upon the population density. (A number of analogous examples are treated from a different angle in Section D 1.) It may be noted also that the density dependence of biotic factors may be so slight as to leave them practically density-independent. For example, the attacks of a polyphagous predator upon a particular population may depend on the availability of alternative prey species, and scarcely at all upon the density of the population in question.

A thorough analysis of any situation would probably have to go beyond a simple division into density-independent and density-dependent factors, and consider degrees of density dependence. Nevertheless, the simple distinction is a very valuable working method, as shown, for example, in the investigations of Errington (1945) on the bobwhite quail.

Density-dependent action is exemplified most clearly by certain biotic factors. Howard & Fiske (1911) considered that parasites were the chief density-dependent factors controlling the numbers of insects, and Smith (1935, p. 890) held that 'entomophagous insects would have to be ranked at the head of the list in general, although in certain specific cases infectious and contagious diseases would precede them'. The natural enemies and pathogenic organisms whose density-dependent action is most pronounced are those which depend wholly or mainly upon the population for hosts or prey. Such enemies tend to affect a greater proportion of the population as it becomes denser, since they are able to find victims more easily and furthermore (in many cases) are thereby enabled to increase in greater proportion than the increase of the host or prey (see, for example, Gause (1934) and Smith (1935) on experimental studies of the relationship between the fly *Phormia groenlandica* and its parasite *Mormoniella vitripennis*, and De Bach & Smith (1947) on the relationship between the same parasite and *Musca domestica*).

Another type of density-dependent action (since we do not propose to restrict the term to mortality factors) is that due to *activities* of the population itself. Under crowded conditions, the mutual interference with feeding, mating and oviposition, and the metabolic effects of continual stimulation, tend to reduce the output of fertile eggs, the rate of development, and the longevity of animals. Other unfavourable activities, such as cannibalism and all forms of intraspecific competition, tend to be intensified as density increases (see Chapman, 1928; Stanley, 1932, 1938; Park, 1932, 1933, 1934; Chapman & Baird, 1934; Crombie, 1943; and others, on cannibalism in *Tribolium*). Mutually aggressive behaviour tends to appear at high densities among mammals, for example lethal fighting occurs in dense laboratory populations of voles (Elton, 1942, p. 205) and is responsible for a high mortality in dense natural populations of muskrats (Errington, 1946, pp. 152–3). Intraspecific aggression appears even at apparently low densities among some of the birds which maintain exclusive territories.

Density-dependent action also arises when some of the things needed by the population are in limited supply. Food-supply, when it is not much greater than the needs of the population, becomes less adequate as the density increases; the denser the population, the smaller is the share of food per individual. This is partly a numerical relationship, and partly due to the reduction of the total food supply by the population. Similarly, space may become a limiting factor as the density increases (cf. Smith, 1935, p. 890). But while the density-dependent effect is brought about by the action of the population in depleting the supply, this could not occur if the supply were much greater than the needs of the population. Hence the limitations of the environment play a part in the process. (It will be convenient to refer to such factors as *supply factors*.)

Finally, a common type of density-dependent action arises from changes brought about in the physical environment by the population itself. They include what is usually called 'conditioning', i.e. contamination of the environment by excretions, secretions, decaying bodies, and carbon dioxide; also changes in the temperature or humidity brought about by the animals. The denser the population, the more marked do such changes become, and any harmful effects on the population are intensified (e.g. Park, 1938). The influence of various animals upon the vegetation, the soil, the aquatic environment, etc., is often considerable, and raises many economic problems. Such modification of the environment is recognized as an important element in ecological succession and related changes (e.g. Fuller, 1934; Hutchinson, 1941). Of course, populations often influence the environment in a way beneficial to themselves. Summarizing this matter in his review of density effects, Hammond (1938, 1939) wrote: 'On the credit side of the ledger, it has been shown that in such diverse forms as protozoa, crustaceans, worms, marine and fresh-water fish, and amphibians the formation of groups may be a protection against toxic substances dissolved in the liquid medium, the presence of noxious solids, extremes of temperature, and other elements of bad environment. Under certain conditions a group of these animals may bring the medium more nearly to optimal conditions or perhaps contribute some important substance to it

and so increase their own rate of growth or reproduction. Increasing population density up to a certain point has been shown to increase the longevity of *Drosophila* and to increase the net rate of reproduction of *Tribolium*.'

Modifications of the environment may be favourable up to a point, and then become unfavourable. Oxley & Howe (1944) and Wilson (1946) showed that insect populations in bulk grain cause a persistent rise in temperature. This change is at first favourable and enables the insects to multiply more rapidly. But when the temperature passes beyond the optimal level, conditions become progressively unfavourable, and finally the insects die out or migrate to the surrounding grain.

The prevalence of density-dependent effects arising from mutual interference, and of those due to modification of the environment, has been established by a large body of work, chiefly on insects and micro-organisms. The results and conclusions have been discussed in reviews such as those by Allee (1931, 1934*b*, 1941), Ford (1937), Hammond (1938, 1939), MacLagan (1941) and Park (1941), and in shorter reviews of special aspects in many research papers.

In the above treatment of density dependence and density independence, emphasis is laid upon them as *processes*, involving the population as well as the factors which act upon it. This procedure differs widely from that adopted by Voûte (1943), who has put forward a scheme of classification of the 'resistance factors' (i.e. unfavourable factors) affecting insect populations. Voûte first divides all resistance factors into two groups: (A) factors which influence all members of a population, physiologically (e.g. temperature); and (B) factors which influence only certain members, 'mechanically' (e.g. parasites, predators). Then each group is subdivided into: (I) factors completely independent of density, (II) factors whose effect on the population depends on its density, and (III, in group B only) factors whose own development, as well as their effect, depends on the population density (e.g. monophagous parasites). Group B I is further subdivided. The result is a complicated scheme, which seems rather arbitrarily constructed, and is difficult to use. It is doubtful whether such a classification justifies itself. The scheme and its attendant terminology may be seen in use in a recent discussion on control (Voûte, 1946).

(*c*) *The form of density relationships*

If we wish to make a more precise study of density-dependent processes, we are faced with some uncertainty about the scope of the term. As indicated below, it might be taken to apply broadly to a whole class of processes, or strictly to one particular type. To avoid confusion, it will be best to use other terms in defining these categories.

The widest reasonable extension of the term density-dependent would cover the whole class of what will now be called *density relationships*, i.e. all relationships which are significantly influenced, directly or indirectly, by the density of the population.

As noted already, a density relationship may operate only above or below a certain threshold level of density. Alternatively, it may be in force at all densities. In either case, within its range of operation, the intensity of action of a density-related process either increases or decreases as the density rises.

Thus we may distinguish between (*a*) *concurrent* density relationships, in which the intensity of the action rises as density increases, and falls as density decreases, and (*b*) *inverse* density relationships, in which the intensity of the action falls as density increases, and rises as it decreases. It is important to note that, in making this distinction, we are referring to the intensity of action *per individual* member of the population, or to the *proportional* effect on the population as a whole. A predator species may kill more and more individuals as the population increases, but if it does not kill an increasing *proportion* of the total population, then its action is not concurrent. If the proportion killed decreases as density rises, the action is inverse. (If it remains constant at all densities, or varies independently of density, the action is density-independent.)

The term density-dependent, in the moderately restricted sense implied in earlier pages, is synonymous with the term concurrent; i.e. they both cover the processes associated with typical parasites and predators, disease organisms, cannibalism, competition for space and food, and modification of the environment.

While *inverse processes* seem to play a much less important part in population dynamics than do the concurrent types, they are worthy of some attention. An example of an inverse process is to be seen when there are insufficient encounters between the sexes to provide for prompt mating, or to provide for the frequent recopulations required to secure a maximal egg-output in certain insects such as *Tribolium* (Park, 1932, 1933); the degree of sex isolation is inversely related to density. Again, many birds which feed on a number of insect species do not increase their consumption of any one species as its numbers increase, or at least not in proportion to the increase in numbers (Tothill, 1922). Hence the percentage mortality due to such a factor declines as population density increases (cf. Nicholson, 1933, p. 171; Smith, 1935, p. 889). The same thing happens even with predators or parasites living on the one species exclusively, provided their rate of increase is relatively slow and their individual capacity for attack is sufficiently limited.

Thus Tinbergen (see Hartley, 1947) found that the intensity of predation by hawks on passerine birds was concurrent, within certain limits; but when the prey species was increasing much more rapidly than the predator, the effect of the latter was proportionately smaller, although the prey density was higher (cf. Flanders, 1935).

The action of any unfavourable processes which are inverse will decline as density increases. Together with favourable concurrent processes, their effect is opposed to that of most density-dependent factors.

What can be said concerning the quantitative aspects of relationships between density and the performance* of populations? One of the assumptions on which the logistic law of population growth is based is that the rate of increase is an inverse linear function of the population density (cf. Smith, 1935; Crombie, 1945). The same assumption is made by Volterra (1926). In laboratory populations, such as those of certain insects which have been studied from this point of view, there is sometimes an inverse linear relationship between density and an aspect of performance or some activity which has been measured (Park, 1933; Chapman & Baird, 1934; Stanley, 1941; Crombie, 1943, 1945). But this is far from being a general rule, and many other types of relationship have been found in experiments of this sort. The analysis of these relationships, the fitting of curves to the data, and the interpretation of the results in biological terms form an interesting offshoot of the main problem of natural control.

For natural populations, however, no simple relationships are likely to be traceable, or even to exist, in a precise or constant form. We have to deal with relationships as they appear in variable conditions, and as interdependent parts of dynamic complex. Yet density relationships undoubtedly exist under such conditions, and they have been demonstrated by quantitative data in a few cases. We need many more data of this sort. Of course, there are many difficult problems associated with getting quantitative data, in a form suitable for the purpose, and with analysing them successfully, and the development of this subject depends primarily upon investigators who count such problems among the attractions of the study of natural populations.

(*d*) *The causes of density dependence*

(1) *Limited capacity of the environment*

The fact that the environment participates in density related actions is obvious enough, for the majority of density dependent factors are physical or biotic environmental factors. It is also clear that any density relationship is subject to the modifying influence of the rest of the ecosystem; for example, mutual interference in crowded conditions is likely to be greater when the temperature is high.

That this is not the full extent of environmental participation in density relationships follows readily from the foregoing passages. We have seen, for example, that the amount of modification of the environment by a population is density-dependent, and reacts back upon the population accordingly. It may also be noted that the degree of shortage of food is density-dependent, and this applies equally to space or any other supply factor. The density dependence arises both from the automatically reduced share per individual when there are more individuals, and from the action of the population in reducing the total supply. Even in the case of mutual interference due to crowding, the environment plays an essential part by restricting the free expansion of the population.

In fact, a fundamental reason for all the above types of density-dependent actions is the *limited capacity of the environment* to maintain large numbers of the species concerned. The capacity of an environment with regard to a species would be measured by the overall density or total numbers of that species which the environment could support. The capacity of an environment is different with respect to different species, and for any one species it changes with the variations of the environment. It may be reduced or increased by the population itself, as when the total food supply is depleted or the environment favourably modified.

The limiting effect is not imposed suddenly and rigidly at a fixed level of density, but gradually and flexibly and in relation to an upper limit which varies. The controlling factors concerned are density-dependent in their action because the limitations of the environmental capacity affect the population in some degree even when the environment is far from being fully occupied. For example, if space or food supply are limiting factors, the share per individual may be more than sufficient up to a particular level of density, then gradually recede from optimum as density increases, until the absolute minimum necessary for survival is reached. (But there is usually a tendency at suboptimal levels of supply for some individuals to get an adequate share while others do poorly and perhaps fail to get enough for survival.) Some of these effects may be found even at the lowest densities, though most operate only above a certain threshold. All of them tend to operate more intensely as density increases. In other words, the more nearly the capacity limit of the environment with respect to a particular species is approached, the more density-

* 'Performance' will be used in a broad sense, including both the level of density and the current rate of increase or decrease of a population. Either of these alone, or the rates of development, reproduction or survival, are *aspects* of performance.

dependent factors come into operation, and the more intensely do they bear upon the population.

We shall see later how the remaining types of density-dependent action can also be related to the concept of capacity.

There is an obvious relationship between the idea of environmental capacity and the 'carrying capacity' idea of Kalabukhov, Errington and others, and the closely related idea of overflow from favourable niches, stressed by Thompson and by Smith (see section B). Whether or not we accept the hypotheses of all these writers in the precise forms in which they presented them the fact remains that the general principle of which they are examples is fundamental to natural control.

One aspect of capacity, the food supply, links the theory of control with what Lindeman (1942) called the trophic-dynamic aspect of ecology. This is the study of the energy relationships between the successive levels in the 'Eltonian pyramid' or food chain, in which plants constitute the 'primary producers', supplying food to the phytophagous animals ('primary consumers'), which in turn supply food for their enemies, and so on. There is a loss of total available energy as the scale is ascended (cf. Macfadyen, 1948).

(2) *The significance of competition*

Intraspecific competition is a natural activity relationship arising from the limited capacity of the environment—particularly as the density approaches the capacity limit. The term competition commonly includes (*a*) direct active struggle between individuals or groups; (*b*) 'a more or less active demand in excess of the immediate supply of material or condition on the part of two or more organisms' or 'the attempt to secure more than a proportionate share of a limited supply of something, e.g. raw materials, food, space or material for construction' (Clements & Shelford, 1939); and (*c*) the occupation or consumption by earlier arrivals of something in limited supply, so that late-comers are automatically excluded or deprived.

For our present purposes, the interesting point about competition is that whenever it occurs it is almost inevitably density-dependent. The amount of space, food, etc. available per individual diminishes as the population density rises, and any competition for them becomes more intense. There are no doubt exceptions to this, such as examples of competition of one type being superseded by responses to more urgent requirements at higher density, but these are minor considerations.

Competition is sometimes wasteful, in the sense that fewer individuals survive on a given supply of food (for example) than could be reared upon it if there were no original overcrowding nor struggle. However, this is only likely to be important in control when food supply is a 'key' controlling factor.

Interspecific competition also plays some part in control. The competitors of a species are those species whose habits resemble its own in one or more respects, i.e. whose needs overlap its own (cf. Crombie, 1947). In competition for a supply of something, the competitor populations are equivalent to extensions of the population studied; individuals of a competitor population are equivalent to a variable number of individuals of the population studied. The presence of competitor species intensifies the density-dependent action of supply factors just as if the density of the population studied were higher than it actually is. Their presence forces down both the upper and the lower limits of its range of variation. They represent a reduction in the effective capacity of the environment.

Special importance has been attached to the process of competition by some writers on control, especially Nicholson (1933), who regarded it as the essential element, without which natural control could not be maintained. However, Nicholson used the word in a much broader sense than is usual; e.g. (p. 140) 'Many organisms alter the chemical and physical nature of their environment, and, generally, the increase in density of such organisms causes the character of the environment to become progressively less suitable for themselves. This clearly is a form of competition....', and again (p. 135) 'If the severity of its action against an average individual increases as the density of animals increases, the decreased chance of survival, or of producing offspring, is clearly brought about by the presence of more individuals of the same species in the vicinity. This can only mean that the decreased chance of survival is due to increased competition of some kind.' The second passage contains the key to Nicholson's idea of competition: it is essentially a statistical conception. What he means is not competition as understood by most biologists, but a broader and more generalized relationship, covering all cases in which the presence of other individuals leads to a decreased chance of survival or a reduced rate of increase, per individual. It is, in fact, any unfavourable density-dependent relationship.

(3) *The density-dependent influence of natural enemies*

As noted earlier, a natural enemy is density-dependent in its action on the host population because it finds hosts (or prey) more readily when they are dense. Of course, if the host population is doubled but the enemy takes less than twice the former number of victims, then its action is not density-dependent;

the density relationship is not concurrent, but inverse (cf. p. 13). To be density-dependent, the enemy must take a greater proportion of the population as the host density increases.

In other words, to be density-dependent, the enemy must respond to changes in the numbers of the host (cf. Nicholson, 1933; Varley, 1947). The nature of this response is commonly twofold. First, there must be a *functional* response to (say) an increase in the host density, because of the increased availability of victims: as host density rises, each enemy will attack more host individuals, or it will attack a fixed number more rapidly. A frequent, but not invariable result of this is an increase in the numbers of the enemy (a *numerical* influence), due to an increased rate of survival or of reproduction, or both; this may or may not be sufficient to produce an increase in the *proportion* of enemies to the increasing hosts.* The numerical relationship is most important when the enemy develops rapidly and passes through several generations to each generation of the host, as do many parasitic insects (Flanders, 1947).

Many natural enemies concentrate in places where the host or prey is dense, thereby showing a more emphatic density dependence than would otherwise be possible. This resembles a functional response when the movement takes place within the environmental limits, but is more like a numerical response when there is immigration of enemies. Richards (1940) wrote that the parasites of the small white butterfly (*Pieris rapae*) 'show a tendency to congregate in the areas where the host is most numerous. This may have a buffer effect on the population, hindering both complete extinction and too rapid multiplication of the host'. If so, it is a reinforcement of the buffer effect characteristic of all density-dependent enemies, whether they congregate or not, and characteristic, in fact, of density-dependent processes of all sorts.

It will be recalled that Nicholson (1933) distinguished clearly between control by enemies and the other types of control, which he attributed to intraspecific competition. Control by enemies, he pointed out, depends on intraspecific 'competition' among individual enemies in searching for victims, or, as he repeated in more clearly statistical terms, on the readiness with which the enemies can find the hosts. Again, it must be remarked that many of the relationships which make the action of enemies density-dependent cannot be described as competition in the usual sense. For example, in the case of pathogenic micro-organisms, there is an increase in the frequency of contacts between host individuals as host density rises, i.e. an improvement in the supply of hosts. The micro-organisms are thereby distributed more readily from host to host, and so tend to increase in relative numbers. Here there is no question of active competition nor of active seeking for hosts. The micro-organisms simply take advantage of the improved capacity of their environment to support their rapid multiplication. Even a virus can react in this way. Yet we have a genuinely density-dependent relationship.

As with the other types of density-dependent factors, we may relate the density-dependent influence of natural enemies to the limited capacity of their environment. Like other populations, that of an enemy species is limited by the capacity of its environment. In this environment the population of the host or prey is an important element. The host population density determines to some extent how readily the enemy can find the victims necessary for its survival and success. Hence inevitably the host density influences the intensity of the enemy's attack upon the host population.

(4) *Density dependence and capacity: Conclusions*

The limitation of populations is a result of the limited capacities of environments. The effects of limited capacity operate even when the density is considerably below the capacity limit, but becomes stronger as density increases.

The ways in which the density dependence of different types of factors is related to environmental capacity may be summarized as follows:

(1) The type of density-dependent effect in which capacity seems to play the least part is *mutual interference*. Yet this is due to crowding, arising from the fact that the amount of space in which conditions are suitable, is limited. Obviously, the interference will increase as density rises. It may be regarded as competition for supply factors.

(2) Other density-dependent factors clearly depend, not on density alone, but on the relationship between abundance and capacity. The total *supply* of food or space is an aspect of capacity. The amount available per individual depends both on the density and on the total supply. A reduction in this aspect of capacity, without change in numbers, or an increase in numbers without any change in capacity, would have the same general effect—an intensification of the density-dependent action.

(In the above types of density dependence, we have a simple combined action by the population and the environment together. In the following sorts of density dependence, there are two distinguishable aspects, first a density-related effect of the population on the environment, and secondly a correspondingly density-related action of the environment back upon

* Varley (1947) proposed to distinguish parasites and predators from other density-dependent factors by calling them *delayed density-dependent factors*. But there is no essential delay in the *functional* response of enemies to changes in host density.

the population. The density relationship may be regarded as being reflected back to the population from the environment.)

(3) *Enemies:* If an enemy is sufficiently dependent on the population as a supply factor, its success in finding hosts or prey will vary according to the population density, and further, if it is sufficiently responsive to such variations, the proportion of the population attacked will increase concurrently with density. Thus the effect of host density on the enemy is reflected as the density-dependent effect of the enemy on the host. But this is possible only if the population is to some extent needed by the enemy for its maintenance, only if the limited supply of this species is (for the enemy) one of the more pressing aspects of the limited capacity of the environment. In other words, the host or prey is a density-dependent supply factor for the enemy (cf. Varley, 1947).

(4) *Modification of the environment by the population: Unfavourable* modification represents a reduction in one or more aspects of environmental capacity, the extent of the reduction increasing concurrently with density. The result is an increase in the intensity of the relevant density-dependent actions.

Favourable modification represents an increase in environmental capacity concurrent with density. Such action is opposed to that of the other density-dependent factors.

In addition to these density-dependent relationships, the presence of *competitor species* reduces the effective capacity of the environment for the population concerned. We shall see later (p. 18) that the presence of alternative hosts or prey for its dependent enemies may have a similar effect.

C4. Phases of control

So far we have referred to natural control as a single process, the result of density-dependent actions. The present section considers its major component elements, and the part played by density-related processes in each of them.

(*a*) *Limitation*

The chief effect of the density-related processes which bring about control, particularly of their property of intensifying as the population density increases, is to 'head off' each rise in density and bring it to a halt. Indeed, since the complex of forces is in a state of continual activity, and for other reasons to be examined shortly, the reversal of an increase often comes rather abruptly. Generally, the higher the density, the more likely is a rising trend to be soon reversed. Thus there is an upper limit, however vague and variable it may be, to the density of each population. The whole process by which populations are 'kept down' may be referred to as *limitation*.

Perhaps the simplest examples of limitation are those in which a population appears to limit itself. This is often due to unfavourable effects of the population upon the environment, a type of phenomenon to which reference has been made earlier. In some cases, a single unfavourable effect alone seems to be immediately responsible for limitation. Thus McKenzie (1943) found that a species of the scale insect *Matsucoccus* on *Pinus ponderosa* had very few enemies, the limiting factor being mortality due to the killing of the branches by the insects themselves as the local density increased.

Unfavourable influences usually affect the rate of development and reproduction, as well as increasing the mortality rate. Because many populations which maintain a very high reproductive rate seldom reach correspondingly high densities, it is widely considered that mortality is by far the more important of the two (cf. Smith, 1935, p. 881). Darwin (1859) remarked that the relative abundance of species of birds or of insects seemed not to be correlated with the number of eggs laid. Nevertheless, a change in the reproductive output of a particular species may have a considerable effect on its density, as in the case of the short-eared owl, cited by Elton (1927, p. 141). Thus changes in the influences affecting reproduction may often be important (cf. Boyce, 1946, on *Tribolium*). Some outbreaks of pests seem to be due largely to this cause.

The density level at which a factor can limit a population is a feature of some practical importance. As pointed out by Smith (1939; and cf. Nicholson, 1933): 'A parasite...in order to be effective must have the ability to find and destroy the surplus progeny of its host at a low host density, whereas an ineffective parasite can accomplish the same thing, but only at a high density.... For this reason the searching ability of the parasite becomes a matter of prime importance, far outranking its reproductive capacity, since the latter is usually, if not always, more than ample.' The elements which affect the power of host discovery by parasitic Hymenoptera were discussed by Flanders (1947). The following paragraph from his paper notes an interesting development of the above point:

'Muir (Williams, 1931) states that: "Theoretically, other things being equal, a predator should be more valuable than a parasite, because the latter only kills a single host or a small number of the host, but a predator generally destroys a large number during its life." Paradoxically, as pointed out by Smith (1937), it is this fact that makes the predator less efficient than the parasite as a control factor. Other things being equal, the most effective species of natural enemy is one that requires the least amount of food for

individual development.' This is supported by the fact, noted by Flanders, that in most groups of insect pests, parasites have been more important than predators in biological control. Other papers dealing with the relative effectiveness of insect parasites and predators are those by Thompson (1929*a*) and Ullyett (1938).

As always, we must bear in mind that there are usually many factors simultaneously active, and that each of them modifies the action or the results of others. For example, animals succumb more readily to disease if their food is deficient, and more readily in some physical conditions than in others. The capacity for reproduction and survival depends upon the physical environment as well as on the inherent qualities of the species. Moreover, a combination of two or more factors may produce a limiting action which they could not exert singly.

As is well known, the mode of control tends to change during the development of an animal, some factors having different effects upon successive developmental stages (cf. Holdaway, 1932), some operating only at an early stage of growth, others only at a later stage (cf. Bodenheimer, 1938; Thompson, 1939; Schwerdtfeger, 1941). For this reason, among others, the importance of a control factor cannot be correctly estimated simply from the numbers of animals killed by it, nor from the percentage killed. The assessment of the real control value of two or more factors operating successively is a special problem which has been studied by Thompson (1928), Bremer (1929) and Bess (1945). Thompson and Bremer assess the contribution of the separate factors towards reducing the population to the level of the previous adult generation. Thompson calculates the 'indispensable mortality', i.e. the percentage reduction due to a factor over and above that which it is calculated the other factors would have produced without it (cf. Parsons & Ullyett, 1936). Bess estimates for each factor the proportion by which it reduces the surviving population. He points out that in one generation of a fecund species, a kill of 5% of the original population may be unimportant if only 50% have been killed by other factors, but very important if 90% have previously been killed. Although the later factors may kill only a small proportion of the original population, yet, if their density dependence is sufficiently marked, they may play a decisive role in regulating the population density from generation to generation. Nicholson (1933, p. 136) went so far as to write: 'If an attempt be made to assess the relative importance of the various factors known to influence a population, no reliance whatever must be placed upon the proportion of animals destroyed by each. Instead, we must find which of the factors are influenced, and how readily they are influenced, by changes in the density of animals.' While the second sentence is the kernel of the matter, a study of the proportions killed by these factors under various circumstances is the chief means available for discovering their degree of density dependence. Analogous considerations apply to density-dependent factors which are not mortality factors.

An important development in this field is the experimental attack upon the problem by Smith & De Bach, working with citrus scale insects and their parasites. One of their methods is to exclude parasites from sections of the scale population by means of organdie sleeves (Smith & De Bach, 1942). The other is to eliminate insect parasites or predators in certain plots by application of selective insecticides (De Bach, 1946). In either case, the comparison of the densities with and without enemies provides a valuable index of the effectiveness of the enemies.

Different factors do not necessarily work in co-operation. For example, if natural enemies keep the population density at a moderately low level, other influences such as food- or space-shortage or disease may not come into operation. In this way the population may be saved from the more drastic reduction it would probably suffer if these factors became operative. Or again, a physical change which reduces the population may operate even more effectively against an enemy. Varley (1947, p. 179) has given numerical examples showing how the destruction of insects, some of which have been parasitized, may lead ultimately to an *increase* in their numbers, because of the greater effect of the mortality upon the parasite species (cf. Nicholson, 1933, p. 151). Taylor (1937) described a striking example of how one enemy may indirectly prevent effective control by others: in Fiji, the coconut leaf-mining beetle, *Promecotheca reichei*, was normally kept under economic control by indigenous parasites; but when the mite *Pediculoides ventricosus* appeared in Fiji, it periodically eliminated all but one of the developmental stages of the beetle; under these conditions the native parasites, needing 'multiple-stage' populations of their host for continuous multiplication, were no longer able to control the beetle, which then became a serious pest.

A population may be affected in the same way by the presence of alternative hosts or prey for its enemies as it is by competitor species. Suppose a controlling enemy is capable of keeping the *total* population of its hosts or prey about a certain level. Then if another species provides (say), half the enemy's requirements, the population studied will be only half as abundant as it would be in the absence of the alternative host or prey—at least this will be so if the enemy is the only controlling factor acting at such levels of density.* Many related questions, such as what may be ex-

* But if the enemy, because of ample alternative hosts or prey, comes to be no longer significantly dependent on this particular species, the action of the enemy upon it will cease to be density-dependent.

pected to happen when there are several competitor enemies, what is the effect of hyperparasites or predators of an enemy, and so on, were considered by Nicholson (1933) and, in a more formal mathematical way, by Nicholson & Bailey (1935). While predictions of this type are likely to be upset in the complex conditions of nature, they suggest useful hypotheses for the investigation of natural populations (cf. Varley, 1947).

The relative effectiveness of a single enemy species as against two or more is a question of some economic importance. While instructive general discussions and theoretical studies are available (Thompson, 1923, 1929*b*; Smith, 1929; Volterra, 1926, 1931, etc.; Nicholson, 1933; Nicholson & Bailey, 1935), no simple comprehensive answer is possible. The evidence from theoretical considerations and from practical experience suggests that the use of several enemy species together is often the better course (e.g. Clark, 1934). Smith pointed out that control by several enemies tends to be more reliable than that due to a single enemy, for any failure of one of them tends to be compensated by an increased effectiveness of the others, in response to the higher host density.

The compensation principle, which applies very generally, is an expression of the fact that if one limiting factor fails, others are called into play by the higher density, while if the numbers are unduly reduced, density-dependent factors operate less severely. The significance of such 'intercompensation' in the control of vertebrate populations has been discussed by Errington (1946). Its importance in connexion with insect populations has often been remarked (e.g. Nicholson, 1927; Thompson, 1928; Bremer, 1929), and is most obvious in cases where a succession of control factors is known to operate. Compensation is obviously important in the practical control of pests, and in relation to the maximum 'catch' which can be taken from a population without detriment to the subsequent yield, as in fisheries.

Limitation is often complicated by seasonal changes. In climates with a marked seasonal cycle, the factors limiting a population are likely to be different at different times of the year. The effective limitation may even be confined to a few months in each year; but it cannot be assumed that the elimination of the bulk of the population represents the essential part of the process. As has been mentioned above, the final small losses may have decisive importance.

If in one season or generation there is a failure of the normal limiting processes, there will be an unusually dense population in the following season or generation. This often provokes limiting processes of corresponding severity.

(*b*) *Suppression*

We must now consider the existence of a time lag in density dependence. As population density increases, the intensity of action of a limiting factor responds by a progressive intensification. This response is not necessarily instantaneous; its promptness varies according to the type of factor and the type of population. The intensity of overcrowding effects may approximately correspond to the density at the time; but the intensity of the effects of a natural enemy may correspond less to the current host density than to the host density a generation (of the enemy) earlier. As we saw above, the first response of a density-dependent predator or insect parasite to increased host density is functional, i.e. there is a more or less immediate increase in the intensity of attack by each individual enemy. This is likely to be followed later by a rise in the numbers of the enemy, due to increased survival and reproduction rates in the presence of a more easily found supply of hosts or prey. So long as host density continues to rise, the fact that part of the response is delayed does not fundamentally affect the relationship or its results. But when the host increase ceases, the effects of this delay may be of great importance, as will be shown below.

If there is little or no delay in response by the limiting factors, and there is an adequate food supply and steady physical conditions, a population may reach the limiting density and maintain itself near that level for some time. But if there is a delay of (say) a week in the response of one of the limiting factors, then, when the density increase comes to a stop, the intensification of the action of this factor will tend to go on for another week. While it may not reach the intensity it would have reached in that week if host increase had continued, it will certainly exceed the value it had when the host increase was brought to a standstill. Hence it will bring about a decline in density (cf. Nicholson, 1933, p. 161). Furthermore, the same delay in response which occurred during host increase will tend to continue during host decrease, but the intensity will be continually *above* the value corresponding to the current host density, instead of below it.

The forced decline in density caused by this excess intensity may be called *suppression*.

Sometimes the forced decline may go on until the population is exterminated as, for example, in the 'relaxation fluctuations' studied by Gause (1934), in which a prey population in the presence of a predator population goes through a cycle of increase, decline and extinction. But other factors may intervene to prevent this. For example, in some of his experiments with *Didinium* preying on *Paramecium*, Gause was able to prevent the complete extinction of the prey by providing some protective cover.

Suppression by enemies is also countered to some degree by density effects among the enemies. For example, Flanders (1935), Salt (1936) and De Bach & Smith (1947) have shown that insect parasites suffer a reduction in their reproduction rate at high density. This would seldom have important effects on the density relationship between parasite and host while the host density is high; but if enemies rapidly reduce a host population and then become concentrated at high density on the surviving groups, the enemies may suffer any of the usual effects of overcrowding in full degree, particularly of course a shortage of food or hosts. Special mention may be made of superparasitism. Flanders (1947) wrote: 'So efficient is the searching capacity of the individual hymenopteron that the survival of many species appears dependent on the fact that the searching activities of the individuals of a population are unco-ordinated. Overlapping and duplication of individual action (superparasitism) tend to preclude the general extermination of the host (when not general, extermination is temporary) and thus insure a continuity of hosts available for oviposition'. Ullyett (1945) found that when the numbers of the parasite *Microbracon* were unduly high in relation to those of its host (*Ephestia* larvae), the numbers of parasites were reduced by superparasitism.

These hindrances in the way of suppression by enemies tend to prevent a persistence of the excess intensity and of the corresponding decline in density. A more general counter-effect to suppression of all sorts is the relaxation,* as density falls, of the totality of density-dependent actions, leaving a larger and larger gap to be filled by the excess intensity if suppression is to go on. Only if the excess intensity is particularly great and persistent can the density be forced down to a level approaching zero.

The above type of suppression, arising from the delayed response of a factor to the density, may be produced by predators, parasites or pathogenic organisms.

There is another sort of suppression which affects aggressors rather than their victims. When the food supply (plants or prey) is readily accessible, but limited, the intensity of food shortage increases relatively suddenly and rapidly as the supply approaches exhaustion. What remains is hopelessly inadequate for the size of the population, which therefore becomes reduced, more often by indirect effects of food-shortage than by actually starving to death; but meanwhile the animals search very intensively and consume all the remaining food which can be found. Thus the supply of food has no opportunity of increasing until the population feeding upon it is reduced to a very low level. Under stable environmental conditions, there might possibly be a balance between a growing food supply and a steady population consuming, so to speak, all the interest and none of the capital of the food supply. But such a balance would be very easily upset, and generally a much less precise relationship prevails.

A similar type of suppression affects populations which contaminate their environment. Generally, the contamination during a period of increase is not only due to the current or recent population (although that would be sufficient to produce an intensifying effect), but also persists and accumulates from the past. This persistence, in addition to the results of any delayed effects (e.g. of decomposition) causes a forced reduction of the density as in the earlier examples.

This type of suppression occurs whenever something required by the population is in limited supply, provided other factors allow the population to increase to a high enough density, and provided the food, space etc., is at least temporarily destroyed, occupied or vitiated when used.

(*c*) *Conservation*

It has been mentioned that in some cases the suppression of a population may tend to persist until it is nearly exterminated. Moreover, powerful density-independent factors, if sufficiently persistent, may also tend to kill the whole population. Finally, factors inversely related to density operate more severely as the density decreases.

That populations are not more commonly exterminated by these forces is due chiefly to the relaxation of density-related influences as the density declines. Other factors tending to save populations from extinction include the presence of a few protective refuges, the occurrence of superparasitism and of overcrowding effects among enemies (all of these have been mentioned already) and such processes as selection and adaptation. These diverse factors or processes produce a result which is in a sense the opposite of limitation, and which may be referred to as *conservation*.

The relaxation of density-dependent forces at low density applies not only to factors which figure prominently in limitation, but to all influences. Hence, any tendency of suppression to exterminate a population is generally offset, at a more or less reduced level of density, by the relaxation of other density-dependent forces. For example, the effects of contamination of the environment may be partly offset by the ability of the animals to move about more freely, or by the reduction of disease, as the density diminishes. The relaxation takes many forms. For example, animals are less easily found by natural enemies when their density is low. For this and other reasons, an enemy may reduce the density of its host to a certain level and then be unable to effect any

* 'Relaxation', as used here, refers simply to a decline in the intensity of action of a factor upon the population, and no connexion with 'relaxation fluctuation' is implied.

further reduction (cf. Muir, 1931, on the *critical point of parasitism*). Again, when the density of a population declines, there is less competition for the more favourable niches in the environment, so that all the survivors may find room in the places giving maximum protection from physical rigours.

The last point involves one aspect of the important part played by the heterogeneity of most environments. This heterogeneity helps to ensure that, whatever the general conditions, some part at least of the environment will be able to offer protection and refuge for some of the population.

If the greater part of a population is killed by unfavourable physical conditions, the survivors (unless their success is entirely due to their being in protected situations) will on the average be those which are more resistant to such conditions. Hence, unless the survivors are weakened by continued exposure, it will be more difficult for the unfavourable conditions to exterminate the population than it was to reduce it. It may also happen that individuals which survive long enough may become better acclimatized or adapted.

Another way in which many populations are saved from extinction is through the existence of dormant or otherwise resistant or protected forms, such as overwintering eggs, cysts, pupae, or other hibernating or aestivating stages.

Sometimes a population will temporarily change its habits under severe stress, e.g. it may change its diet for a time while its normal food is scarce (cf. Elton, 1927). Dugmore reported that after a severe reduction of the African buffalo by rinderpest, the remnants of the population in the Sudan changed from diurnal to nocturnal feeding habits, retiring to cover during the day; later reports indicate a return to its former habits after more than 20 years of population increase (Elton, 1927).

To summarize the aspects of conservation, there is a strong tendency for the last remnants of a reduced population to survive the unfavourable conditions; this is due to one or usually more of the following factors, and perhaps to others as well: (*a*) the heterogeneity of the environment and the existence of a few specially favourable refuges, (*b*) isolation and the consequent tendency to escape enemies and disease, (*c*) the occurrence of superparasitism (by parasitic insects) and overcrowding effects among enemies as host numbers fall, (*d*) some other aspect of the relaxation of unfavourable influences which accompanies a fall in density, (*e*) immunity, (*f*) acclimatization, (*g*) selection, (*h*) the existence of a specially resistant stage in the life history, or (*i*) a self-protective change in behaviour.

(*d*) *Release*

It is well known that when a population is severely reduced, any predators, parasites or disease organisms which are more or less wholly dependent on the population concerned tend to be even more severely reduced. One or more of these enemy species may be of major importance in the control of the population. This relaxation of controlling influences is the normal accompaniment to falling density.

But sometimes, and in spite of the processes of conservation which apply to the populations of enemies and victims alike, an important enemy may be locally exterminated. Then the subsequent increase of the host population is likely to be both faster and more sustained than usual, until other factors effect control at a higher level. Or the missing enemy may reappear by immigration, and belatedly set about the process of overtaking and controlling the swelling host population. What is more common is something intermediate between this and the normal relaxation of controls. For example, predators, parasites or disease may be reduced to a few nuclei at low density, so that the host population can often increase again for a time before the normal relationships with these control factors are re-established.

Again, if food supply is normally an important control factor, the extra food which accumulates during a period of low density may allow a rapid subsequent increase to unusually high numbers.

In general, a great reduction in density tends to disorganize natural control, and sometimes a population temporarily escapes more or less completely from one or several of its important controlling agents; this allows it to increase more rapidly than is usually possible for it, at a given level of density, and may allow it to reach a higher density than usual. This phenomenon may be referred to as *release*. The clearest examples of release are to be observed in populations whose control is normally dominated by one or two 'key' factors; in other types of control it is less likely to be important, because of compensatory action by other factors.

(*e*) *Fluctuations inherent in control*

It is interesting to note that two of the aspects of control are such as to promote fluctuations. Suppression promotes downward fluctuations from high density; release promotes upward fluctuations from low density. Of course, in a normally variable environment, even limitation and conservation lead to reversals in the trend of density rather than to steady numbers. Suppression and release are due to more purely biotic forces which may sometimes reinforce and sometimes cancel the more or less irregular fluctuations due to weather, etc.

There is some tendency for release to follow suppression, and vice versa. The existence of a very high density exposes a population to the risk of some suppressive process coming into operation. If this process persists, and forces the numbers down to a

very low level, the likelihood then arises that some parts at least of the population will be temporarily released from the usual controls, and it may reach very high numbers again before being overtaken by control.

An apparent example of suppression following partial release has been observed in the pine moth *Bupalus piniarius*. The fluctuations of this species in a pure stand of its host tree were described by Engel (1942). Under these conditions its natural enemies are less numerous than usual, so that the moth can increase rapidly and reach unusually high densities. But when the enemies finally do overtake it, they cause an unusually rapid reduction in the numbers of the moth.

Reporting observations on a quite different animal, the bank vole, Evans (1942) wrote: 'The population "survival" from a period of high density to one of low density appeared to be greater in those habitats which had normally maintained a low population density. It is suggested that habitats which will maintain only low densities may be essential to the ultimate survival of a species.' In other words, where the density is never very high, the catastrophic effects of violent suppression are avoided.

It is difficult to estimate how far these tendencies are extended towards a series of continuous oscillations in density. Under most conditions, any such tendency would probably be lost among the many other influences at work, such as the effects of weather changes, and all the intercompensatory forces characteristic of normally complex biocoens. The question is further discussed in section D4.

C5. The level of abundance

So far we have discussed the controlling processes by means of which a population is kept within a certain range of density. While it has been convenient and useful to consider control in this restricted sense, most biologists would take a broader view, and think of the natural control of a population as including the determination of the general level of abundance to which the population is confined by the regulating processes. Control in this broader sense may be thought of as a phenomenon separable into the three parts: (*a*) the regulating processes, which we have discussed above, (*b*) the determination of the level of density, and (*c*) the determination of the general level of abundance, which may be defined only after a population has been observed over a period of time. These three sets of processes are not really distinct; each includes a good deal of the other. This is particularly true of (*b*) and (*c*), for the general level of abundance is no more than the actual density over a period, and it must be determined in the same way (or succession of ways). But neither is (*a*) really distinct from (*b*) and (*c*). Thus, although we have so far concentrated upon the controlling processes, this has involved us, for example, in a consideration of environmental capacity. The conclusion we reached may be re-stated in this form; that a population is as big (numerically) as the capacity of the ecosystem allows. Rather more fully: the density of a population is determined by the capacity of the ecosystem to maintain large numbers of the species, and large numbers of its density-dependent enemies. We have also noted some of the factors which determine the level below which a population is limited.

In fact, for a given species in a given environment, it is quite clear that it is the controlling processes which determine the abundance of the population. But in general, we must not take for granted either the characteristics of the species or those of the environment. Then the abundance of a population depends, first, on its own specific characteristics and capabilities, and, secondly, on the general suitability of the environment for the species concerned, i.e. upon physical conditions, and on the quality of the food, as they affect the rates of reproduction and survival. Thirdly, it depends on the amount of space, food, etc., available. Fourthly, it depends on the prevalence and efficiency, or otherwise, of enemies, competitors and diseases. In short, the level of abundance depends on all the major elements in the complete ecosystem.

Many biologists would say that in general one major element, namely climate, tends to play the predominant role in the determination of abundance. According to the nature of the species, there are some types of climates in which it can be abundant when other conditions are favourable, and other types in which it can seldom or never be abundant. The physical conditions in some environments are quite different from the general meteorological conditions, yet are still related to them in a broad way; even the vegetation, which considerably influences the physical conditions as well as dominating the environment in other respects, is itself determined in a general way by climatic influences.

Be this as it may, the abundance of a population depends on all the major aspects of the general environment. More immediately, it is determined by those aspects of the environment which are predominant in control. The *precise* level of density at any time depends on all this and upon many temporary and 'chance' circumstances in the ecosystem at the time.

The question, whether the controlling processes or the environmental background is generally more important in the determination of abundance, is meaningless. And in relation to particular cases, it has meaning only when major parts of the ecosystem are taken for granted. Given a particular population and its general environment (not the immediate control factors) we

may say the control factors determine the level of abundance—as has been shown in practice with various insect pests. But in general we have also to recognize the validity of the complementary proposition: given a population and its immediate control factors, the level of density is determined by the general environment. In fact, all three elements—the population with its specific characteristics, the general environment, and the control factors—together determine the level of density, and while it is convenient in studying actual cases to take one or two of them for granted, the conclusions so reached must not be expected to apply in general.

Consider, for example, a population whose density is apparently determined by parasites. In his interesting account of the natural control of the knapweed gall-fly *Urophora jaceana*, on a site near Cambridge, Varley (1947) provides data showing the effect of the chalcid parasite *Eurytoma curta* on the density level of the fly. Apart from a number of modifying factors whose action is studied, the general effect of climate, for example, is taken for granted. This is natural and inevitable. But Varley makes the generalization: 'Where other factors permit its survival it is the controlling factors which mainly determine whether a species shall be rare or common'. This is correct only if it refers to the immediate or direct determinants of abundance.

The viewpoint of this section is somewhat similar to that of Nicholson (1933, p. 172) on the subject, inasmuch as Nicholson holds that the controlling processes are the immediate determinants of density, the physical environment being the ultimate determinant; for the physical environment influences the controlling processes, besides determining which controlling agents shall be present. Smith (1935) seems to consider the determination of density as part of the regulating processes, except in extreme cases of a shift in the general level, as in outbreaks of a pest. It is partly for this reason that Smith lays more emphasis upon the importance of climatic factors in regulation.

The theory that the size of a population depends on the resultant of the push of 'biotic potential' against 'environmental resistance' is based on a sound idea, but its development by Chapman (1928, 1931) is open to many objections, some of which were referred to by Nicholson (1933) and Thompson (1939). One of its faults is the term environmental resistance, which ignores the important fact that populations to some extent control themselves. The resistance comes from the whole ecosystem, not only the environment. This theory deals essentially with the resultant resistance, measured in terms of the performance of the population. It says nothing about the relative contributions of the interacting elements to the final resultant, though it suggests ways of assessing them.

The immediate determinants of the abundance of a population are not necessarily the same in all parts of its environment. Frequently it is held at a low density over the greater part of the environment, because of exposure to enemies or because tolerable physical conditions exist only in a few niches. But in the more favourable parts it may reach a high density, and be controlled by different enemies, or by exhaustion of food supplies, or overcrowding, or some other factors not operative elsewhere.

On the whole, then, it seems there is no certain basis in present knowledge for any very simple generalization about the determinants of the level of density, except that the immediate determinants are the control factors and the ultimate determinants are all the chief elements of the ecosystem. In particular cases, on the other hand, it is sometimes found that parasites, food shortage, or some other one or two factors, are responsible for setting the general level considerably below that which would otherwise prevail. For example, Hardy (1938) considered the reason for the greater abundance of the diamond-back moth (*Plutella maculipennis*) in New Zealand than in England was the low rate of parasitism in New Zealand, and suggested the introduction of further parasites. This was done and has apparently been very effective in reducing the pest (Anon. 1946). Or (what may be the same thing) a favourable change in a particular factor may allow a considerable rise in density; thus Criddle (1930) reported that maxima in sharptailed grouse populations were due primarily to the periodic abundance of food provided by grasshopper outbreaks.

For particular groups of animals, such as a class of vertebrates, an ecological type of insects, etc., it is possible to establish generalizations of the sort reached by Errington (1946). From his study of predation among vertebrates, he concludes that for birds and mammals 'predation looks ineffective as a limiting factor to the extent that intraspecific self-limiting mechanisms basically determine the population levels maintained by the prey'. In other words, of the environmental determinants the non-predatory elements are the important ones. Even such a general statement is very useful. Generalizations may also be made about particular regions, such as the statement that in general the level of density of populations is relatively low in the tropics, perhaps because of the intense struggle against enemies and competitors (Hesse, Allee & Schmidt, 1937, p. 404).

D. SOME SPECIAL QUESTIONS

In this part of the paper we shall consider several themes which, although important and interesting, are not essential to the conception of control developed in the previous part. Some points of this sort have been dealt with in earlier pages, because it would

have been inconvenient to separate them from the themes discussed there.

D 1. The relative importance of different factors in control

There has been a good deal of discussion for many years as to the relative importance of different factors in control, particularly as to whether biotic factors are more important than physical factors, and vice versa.

In general, the performance of a population depends both on its inherent qualities and on the nature of the environment, and it would be pointless to claim that either is more important than the other. If biotic factors include the inherent characteristics of the population, or its modes of reaction to the environment, we cannot assess their importance relative to that of the physical environment. But can we compare the importance, to control in general, of physical and biotic *environmental* factors?

Taking a broad view, we see that the physical factors provide the environmental climate which influences very considerably the general vigour, the rate of development, the powers of survival and the general level of metabolism and activity of a population. Further, they play the major role in determining whether or not a given species can exist at a particular place, and often in determining the general level of density. This is borne out, for example, by the fact that it has been possible to map the areas of distribution and of mass development of various insects, using meteorological and physiological data; such maps correspond reasonably well with the actual occurrence of the species concerned, in those parts of the world to which they have penetrated (e.g. Cook, 1925; Bremer, 1929; MacLagan, 1932; Zwölfer, 1935; Davidson, 1934; Ullyett, 1936). By comparison, the biotic factors often play a secondary role: even although they may sometimes bring about the extermination of a population, they cannot operate unless the physical conditions are suitable for the existence of the species concerned. Furthermore, biotic factors are always subject to the influence of physical conditions, while the reverse is true only in certain cases (cf. Thompson, 1929*c*). In this sense, the physical factors are of primary importance, the biotic factors secondary.

But if we consider the controlling processes, i.e. the more direct or immediate determinants of density, we are at once impressed with the great importance of the biotic element. A population's own activities play such an important part in its control, and natural enemies are so often important, that we are tempted to rank the living elements as predominant over the physical background. Yet, as we have seen earlier, the general environment enters into all the density-relationships which are responsible for control.

To look at this matter in another way, it is clear that factors do not act independently upon a population. They are parts of a complex system and subject to the influence of the whole. This means, among other things, that the influence of a factor upon a population depends upon other factors. Although this is generally recognized, very few authors seem to have realized its full implications. It applies with special force to the question under discussion, because—to mention only the most striking feature—the action of biotic factors is often influenced decisively by physical conditions.

The effects of a physical change upon the physiological processes of different species are usually unequal and sometimes opposite (and the physical limits for survival are often different for associated species). In many cases these differences have been shown to play an important role in determining the outcome of the population interaction of an animal with a parasite or predator. Such facts have been known for many years, but their significance seems to have been generally underestimated in theoretical discussions.

A number of examples in which the effect of parasites, predators or diseases on insect populations is dependent upon temperature, humidity, or both, were cited by Uvarov (1931, pp. 152–5) and Payne (1934), and others were described by Ullyett (1938) and Pruthi (1940). Ross (1908) stated that the numbers of malarial parasites in man or birds increased with a rise in the external temperature. Ahmad & Ullah (1939) showed that the relative success of the bollworm *Earias fabia* and its parasite *Microbracon lefroyi* were very different under different physical conditions. 'It is well known that the development of aphid parasites is so relatively slow during cool weather that aphid populations often increase enormously before they are controlled biologically' (Flanders, 1947). Holdaway (1932) showed that the cannibalistic limitation of its own species by *Tribolium* was affected by humidity. Beauchamp & Ullyett (1932) showed that the outcome of competition between pairs of species of planarians depended in some cases on the temperature, in other cases on the joint influence of temperature and the rate of flow of the water in which they lived. Hutchinson (1941) discussed some examples showing the important part played by physical conditions in determining which of two or more competing species of micro-organisms become dominant. Ball, Reeves, Boyden & Stone (1935), in an ecological study of the celery leaf tier, *Phlyctaenia rubigalis*, in Florida, 'worked out an extremely complicated biological complex involving 2 host plants for leaf tiers, 3 parasites, several birds, 2 diseases, and a number of predators, all intimately associated in an unstable balance largely influenced by temperature factors.... A fluctuation of 1° or 2° from the normal mean temperature of the 3 winter months... was found to make

the difference between serious infestation and no commercial injury. This almost hair-trigger reaction was the result of a number of interacting factors, the most important being the time required to mature a celery crop as compared with the time required to mature a brood of worms.' It has been found (Solomon, 1946) that populations of the grain mite *Tyroglyphus farinae* in English granaries tend to be severely reduced each summer by the predatory mite *Cheyletus eruditus*, whereas this predator is quite ineffective in the winter. Both species survive the seasonal changes of physical conditions, but their interaction is fundamentally affected.

Failure of an enemy in certain environments is not always due to retardation of its rate of increase relative to that of the host, or to reduced activity; certain physical conditions may bring about a lack of correspondence between generations or emergence of host and enemy. According to Baker & Jones (1934) such disharmony of life cycles has been an important factor in reducing the effectiveness of the parasite *Exeristes roborator* in the control of the corn borer, *Pyrausta nubilalis*, in parts of North America. Richards (1940) states that the life cycle of the parasite *Apanteles glomeratus* is ill-attuned to that of its principal host under English climatic conditions, since a third generation tends to emerge in the autumn, generally in the absence of any corresponding third brood of its main host, the larva of *Pieris brassicae*. The natural control of certain gall midges is strongly influenced by the effect of weather conditions on the rates of development and times of emergence of their parasites, and on the condition of their host plants, in relation to the time of emergence of the midges (Barnes, 1935, 1940).

There is another difficulty in assessing the relative importance of biotic and physical factors in general. In particular cases, our impression of the relative importance of different factors depends a great deal on the relative amounts of variation of each factor, and particularly on the amount of their divergence from the optimum. If physical conditions are steady and favourable, biotic factors may appear to be all-important (cf. MacLagan & Dunn, 1935; Ford, 1937), but if physical conditions are very variable or extreme, biotic factors may seem to be of minor significance. Thompson (1929*c*) concluded that physical control is most effective in regions such as the polar zones, deserts, and other barren places, where physical conditions are unfavourable to life, and least effective in places like tropical rain forests, favourable to life; the importance of biotic factors varies in an inverse manner (cf. section D 5). It must also be borne in mind that the degree of sensitivity to adverse conditions, particularly to physical conditions, may differ a great deal as between species. Some are vulnerable, others hardy; some are strongly influenced by small changes, others seem relatively indifferent to large deviations from the optimum.

It is often possible to pick out one or two 'key' controlling factors, which are chiefly responsible for setting a limit to the density of a species in the areas where it is common. For example, Salt (1932) showed that the enormous potential increase of the sheep maggot fly, *Lucilia sericata*, is offset chiefly by the restricted supply of suitable food for the larvae. The abundance of the lucerne flea, *Smynthurus viridis*, depends mainly upon moisture and temperature (MacLagan, 1932; Davidson, 1934), and that of the mite *Tyroglyphus farinae* on moisture (Solomon, 1946). The work on the celery leaf tier reveals temperature as a key factor in the control of this moth (p. 24). Discussing fresh-water animals, Eggleton (1939) wrote: 'for the bottom dwellers, the character of the substratum on and in which they live is usually of such paramount importance that its effects may completely outweigh the influence of other powerful factors. In the swiftly flowing streams which we are considering this factor vies for first place in influencing the benthos with the ever-present stream characteristic, current....' It should be recognized, however, that such statements apply only to situations in which the other important elements are relatively stable and favourable. Any important part of the whole complex which is outstandingly variable or unfavourable is likely to act as a 'key' controlling factor (cf. Allee & Park, 1939).

Of course, what is termed a 'factor' is largely a matter of convenience, and can usually be analysed into a number of separate elements if its operation is closely studied. Thus 'moisture', as it affects *Smynthurus*, includes soil moisture content (determined by climate, soil type, topography, etc.) and the humidity and evaporating power of the air (Davidson, 1934).

Finally, the question of the relative importance of factors is subject to the difficulties arising from cases of inextricably combined action by two or more factors. For example, suppose a change in physical conditions destroys the local food supply of a population and so causes it to move into another area where, on an inadequate diet, it is unable to escape from a predator species which thus exterminates it. Which is the more important, physical change, food shortage, or predator?

To summarize, it is difficult to say in general whether physical or biotic environmental factors should be considered more important in control, for both are fundamentally involved. But it is often possible to make such a decision with reference to a specified situation. In particular situations, even a single factor, either biotic or physical, may be recognizable as dominating the control of a population. But there is always the difficulty that factors are not

completely distinct from and independent of the ecosystem as a whole.

D2. Balance of populations

The common idea that populations exist in a state of balance or equilibrium is closely connected with natural control. Unfortunately, there has been a great deal of confusion and inconsistency both as to the meaning of the term and the nature of the phenomena it has been applied to. We shall now consider under what circumstances it is appropriate to apply it to populations.

The term is of course borrowed from physics. A body is said to be in (static) *equilibrium* when it is at rest, or has a uniform velocity. The forces acting upon such a body are in *dynamic equilibrium*, i.e. their resultant is zero. An object or system is in *stable equilibrium* insofar as it can return to its former position or state after displacement.

(*a*) *Correct application of the term 'balance'*

Since biological phenomena involve a higher level of organization than physical phenomena, physical terms and ideas apply to them only by analogy. But when such analogies are used, they should be carefully and logically developed, for if they are treated more loosely than need be, confusion is inevitable.

If we are to apply the idea of equilibrium logically to population density, it would seem that a population should be regarded as approaching equilibrium insofar as it approximates to a steady density. This is presumably the conception which Elton (1930) had in mind when he stressed the unbalance or disequilibrium of natural populations. Attempting to generalize the dynamics of the matter, Chapman (1928, 1931) held that the biotic potential ('the inherent property of an organism...to increase in numbers') tends to maintain a state of balance with the resistance of the environment; balance is reached when these two forces are equal, and the population remains steady. Lotka (1925) discussed biological equilibria, and pointed out the proper use of the term as a description of an unvarying state. He remarked that, strictly, a biological equilibrium such as that of a constant population is not true equilibrium, since its steady state is maintained by a continual expenditure of free energy, but he thought it justifiable to neglect this point.

As is well known, populations which approximate to a steady density will return to this level after the density has been artificially raised or lowered. In other words, population equilibrium is stable.

(*b*) *The views of Nicholson and of Smith*

Nicholson (1933) used the term balance in a very different way from that which has been indicated above. He maintained that since the density of a population is related to environmental conditions, changing when they change, the population must be in a state of balance.* If the general environmental conditions are constant, competition keeps the population to a constant density, and a state of stationary balance prevails. Comparing the state of a varying population with that of a free balloon, Nicholson (p. 133) wrote: 'The balloon is continually in a state of tending towards a position of stationary balance, but continues to rise and fall because the position of stationary balance is changing all the time.' In terms of population density, the population is tending all the time to come into equilibrium with the prevailing environmental conditions, but these conditions are continually changing, so drawing the population towards a continually changing equilibrium level.

This use of the term equilibrium is open to serious objections. In the first place, even if we agree that each population continually tends to come to an equilibrium level, it only *tends* to do so, i.e. at the most, it has a *tendency* towards equilibrium. But, says Nicholson, this level towards which the density tends is continually changing. Therefore it is not an *equilibrium* level towards which the population tends. In short, Nicholson's use of the idea of equilibrium seems quite inappropriate, and bound to create confusion.

Yet another viewpoint is that adopted by Smith (1935), who regarded population balance as synonymous with a very roughly steady state, and interpreted all normal fluctuations in density as deviations from a fixed average. He wrote (p. 878), 'there is brought about a kind of equilibrium which, by physical analogy, must be referred to as "stable" as contrasted with equilibria of the unstable or neutral types. This is due to the fact that any tendency of the density to depart in either direction from the average modifies the environmental forces acting on the density in such a way as to restore it to the average. Even extreme oscillation, therefore, does not destroy the equilibrium. Oscillations are the resultant of the forces which adjust the numbers of individuals of a species to the capacity of the environment in which the species happens to exist. This is the characteristic of populations which is referred to by that much misused term "balance of nature".' However, 'temporary displacement of the equilibrium position occurs when a species which is ordinarily of little or no consequence appears in enormous numbers...' (p. 879).

This seems an extremely loose application of the term equilibrium. If we consider that all or most

* Thompson (1939) considered that Nicholson here identified balance with the cause-effect relationship between environment and population, and that he used the term balance in two different senses.

populations are usually in stable equilibrium, it is difficult to avoid the conclusion that most natural phenomena are in the same state. It is necessary to add that Smith is by no means alone in his use of the idea that insect populations exist in a state of equilibrium which is broken only at times of outbreaks (see, e.g. Schwerdtfeger, 1934; Graham, 1939; Voûte, 1946). But it may be that economic entomologists tend to lay more stress than is theoretically justifiable on the difference between the variability of 'normal' and outbreaking populations.

(*c*) *Dynamic equilibrium*

Reference must be made to the idea, widespread among biologists, that while *static* equilibrium involves constancy, a population which varies in response to environmental changes is still in *dynamic equilibrium*. But dynamic equilibrium usually refers to the balance of the *forces* operating upon a body or within a system which is in static equilibrium. The appropriate application of this to population density is, therefore, that dynamic equilibrium is a condition in which the various forces or influences affecting the abundance of a population are balanced, i.e. their resultant is zero, and the population density is constant. If we apply the term balance very loosely then the dynamic balance involved is equally loose; but in no way does the addition of the epithet 'dynamic' make a loose application of the term balance more appropriate.*

(*d*) *Balance between populations*

If two species living together in the same environment each maintain an approximately constant density, and each influences the density of the other in some degree, so that each is somewhat reduced, though not eliminated, by the presence of the other, then we may speak of a balance between the two populations. Some apparent examples of such a relationship are seen in laboratory experiments with micro-organisms (Gause, 1934) and insects (Crombie, 1945). It could scarcely occur in a varying environment.

Certainly, pairs of populations in a natural biocoen often vary dependently. For example, the variations in the numbers of a predator may bear a continuous relationship to those of a particular prey population. But such relationships are usually neither simple or precise enough to make the idea of a balance between the populations appropriate; linked or dependent variation would be a better description.

Lotka (1925) made the point that slowly changing populations which bear an approximately constant relationship to each other, so that they may be regarded as mutually equivalent, may reasonably be said to form a *moving* equilibrium. In his chapter 21, he applied this term to the system comprising the American populations of man, swine, cattle and sheep, which, over several successive decades, increased in roughly equal proportion, governed by the increasing size of the human population. Lotka applied the idea of moving equilibrium only to systems which change very slowly in relation to the time required to restore equilibrium.

In her study of the effect of environmental conditions on the success or failure of the parasite *Microbracon* in controlling the Mediterranean flour moth, Payne (1934) made great use of the phrase 'host-parasite balance'. The analogy implied is with a loaded weighing balance, which tips to one side or the other in a state of *imbalance*. However, since the intention is quite clear, no confusion arises in this case.

(*e*) *Conclusions*

First, to summarize: the application of the physical term equilibrium or balance to a population at constant density involves an appropriate and reasonable analogy. The term is not appropriate to normally variable populations, even if they are regarded as tending towards a varying equilibrium level, or as (very roughly) fluctuating about a fixed mean level. Nor should the epithet 'dynamic' be used as if to indicate that only a loose sort of equilibrium is involved. A state of balance between two or more populations may be said to exist if each is approximately constant at a level of density determined partly by the others.

Perhaps the most practical conclusion to draw is that in view of the confusion arising from the loose application of the term equilibrium, biologists should take care to avoid using it inappropriately; other terms should be used to describe the state of populations varying in density; and finally, whenever the term equilibrium or balance is used in biology, it is advisable to state fully and clearly which forces are involved, and in what the state of balance is considered to consist.

D 3. THE MODE OF VARIATION IN ABUNDANCE

The question of balance is closely related to the way in which population variations are conceived; so indeed is the whole question of natural control, and it

* Another term, *kinetic* equilibrium, is used in physics for the state of *any* moving body, the equilibrium being that between the force of inertia of the body and the forces which give it acceleration (d'Alembert's Principle). The term dynamic is occasionally applied specifically to such equilibrium, but this is unusual. In any case, this sort of equilibrium is shared by all bodies or systems which are neither at rest nor moving with uniform velocity. Hence it is not particularly useful to apply the term in this sense to populations.

is inevitable that the mode of variation should have been touched upon several times already in this discussion. In the previous section, Nicholson's idea, that density tends towards, or fluctuates about, an equilibrium level which varies, was discussed in reference to the concept of balance.

Nicholson (1933) seems to have introduced this idea of variation for the immediate purpose of separating (*a*) the fluctuations of a population about the 'steady density' (the temporary equilibrium position) from (*b*) the changes in numbers due to alterations in the level of the 'steady density' itself. The fluctuations (*a*) are supposed to be due primarily to interactions with enemy populations, while the changes in level (*b*) are due ultimately to the physical environment; the validity of this distinction depends partly upon whether or not it is considered possible to sort out the two kinds of fluctuations. Nicholson's ultimate object was apparently to provide a basis in biological theory for mathematical deductions about population interactions, in which the environment is first assumed to be constant and later introduced as a modifying element. The distinction is of course very difficult to maintain in practice, although Varley (1947) has recently made a beginning in the application of these ideas to a practical problem. It is also interesting to note the parallel with the ecological system of Clements & Shelford (1939); they postulate a primary level of interaction between the living elements of the ecosystem and the physical environment, and a secondary set of interactions between the organisms.

Such a distinction between two types of agents is justified if it is found useful in dealing with mathematical or practical problems. But it does not follow that population dynamics must be viewed exclusively or even predominantly from this angle. I have taken the view that for the purposes of a general theory of control, it is not the most useful line of approach.

We have also referred earlier to the concept that populations simply fluctuate more or less regularly about a mean level of density. Smith (1935, p. 878) writes: 'The general picture of the population changes of a species may. . . be represented as a series of more or less periodic fluctuations of varying intensity about an average density.' This is close to the idea, criticized by Uvarov (1931, p. 161), that variations in population density can be compared to the swinging of a pendulum from side to side of the mid-line. It also has affinities with the mathematical theories of enemy-prey interactions in a constant environment, which envisage the populations concerned as undergoing regular oscillations.

This is much too regular a picture to be generally applicable. Natural populations, on the whole, fluctuate much more violently and erratically, responding not only to changes in associated populations, but to the irregular variations of the physical environment. Many populations fluctuate chiefly within a low range of density, with occasional outbreaks; if we draw in the mean density level on a population graph covering a long-enough period, it is *above* the level of most of the fluctuations. If these fluctuations are related to any mean value, it must be to a lower, temporary one, which is superseded each time there is an outbreak. This is the view Smith adopts. But this is only a special case of a more general difficulty. Many other population curves do not give the least impression that the fluctuations are related to the mean value. Movements towards the mean are often reversed before it is reached. Furthermore, while the idea of fluctuation about a mean may seem realistic when the fluctuations are small compared with the mean value, it is scarcely appropriate to cases in which the 'deviations' are almost as great as the mean value, still less so when some of them are many times greater (cf. Thompson, 1939; Bodenheimer, 1938).

The idea of more or less regular fluctuations about a mean is linked with the conception that each deviation from the average produces forces which cause a return to the average. Certainly, as we have seen, high or low densities do tend to produce conditions causing a return to intermediate numbers, or sometimes to the opposite extreme. But Smith, as in the passage quoted on p. 26, held that 'any tendency of the density to depart in either direction from the average modifies the environmental forces acting on the density in such a way as to restore it to the average'.

To this we must object that there are forces tending to reduce the population even when the density is low, and forces tending to increase the numbers even when they are high. Only, the more extreme a variation becomes, the more is one set of forces strengthened, and the other weakened, until finally the point is reached where the trend of increase or decrease is reversed. When and where the reversal occurs will depend, not on the relation between the present density and the average density, but on the current condition of many varying factors in the ecosystem. Many of these factors are irregular in their variation, yet only within certain limits. Similarly, the density variation of the population will probably be irregular, but only within certain limits, often within the range of a recognizable general level of density. In short, its variation is restricted, it is subject to natural control.

D4. Do controlling processes cause periodic fluctuations?

An explanation of the way in which enemies or food shortage might cause population oscillations was offered as long ago as 1863 by Herbert Spencer in *First Principles*, and a partly speculative example

from populations of Lepidoptera was described by L. O. Howard in 1897 (both quoted by Lotka, 1925). Modern ideas on periodic fluctuations have been considerably influenced by the concept of 'classical oscillations' developed in the mathematical theories of enemy-prey interaction.

When Gause (1934) set out to reproduce 'classical oscillations' experimentally, he found that the natural tendency of the micro-organisms he used was towards 'relaxation oscillations', in which the predator steadily killed all the prey and then died out itself. It was only by carefully manipulating the experiments, or systematically adding to the populations, that he was able to produce cyclic fluctuations. It was easier, by providing a refuge for the prey, to produce a sort of incomplete relaxation oscillation in which some of the prey survived the dying out of the predator and then increased freely.

It may seem, as indeed it is, a long step from these highly artificial experiments to the 10-year cycle in natural populations of the varying hare. Nevertheless, we have seen that MacLulich (1937) considered the fluctuations of the hare populations he studied to be examples of relaxation oscillations of the modified type in which a refuge is available—in this case a means of survival for the 'enemy' (disease organisms) as well as for the prey. While later work (Green *et al.* 1939) suggests that the disease responsible for the decline of the hare populations may be physiological and not infectious, MacLulich's theory at least serves to draw attention to the fact that a series of incomplete relaxation oscillations might be indistinguishable from genuine 'classical oscillations'.

By whatever name we call them, the type of oscillations envisaged by the overpopulation theories of Eidmann, Dymond, Kalabukhov, Clarke and others (see section B4) come into the same general category as the 'relaxation oscillations' of Gause's experiments. The consequences of overpopulation tend to destroy all the animals, but a few survive in protective 'refuges'.

When the crash of a population is apparently due to a particular enemy or disease, the survival of a few nuclei of these appears to be a regular phenomenon.

The recovery of the fluctuating population may be regarded as a reaction to the further reduction of enemies or disease because of the low density of the host, or in some cases perhaps to the development of immunity, and often to changes in weather, etc. After a crash due to food shortage, the food organisms will similarly benefit from the low density of the population, and will normally recover and so make another increase possible. Persistent ill-effects of overcrowding disappear after a period at low density. These matters were discussed in section C4, where we noted a general tendency towards population fluctuations both upwards from low densities and downwards from high ones. As we have seen, this is not confined to interacting populations, but may arise in a population which temporarily uses or spoils its physical environment.

The question, whether we should expect any of these phenomena to produce *regular* oscillations in nature, is a difficult one. It depends on our estimate of the constancy (or regularity) of environments. In this connexion, two general observations seem significant. First, the periodic fluctuations of natural populations are not precisely regular; indeed, in many cases the existence of an element of regularity can be established only with difficulty and over a long period of years. Secondly, most of the populations whose fluctuations are the most strikingly regular live in the far north, where the environment may be regarded as unusually uniform (Dymond), and unusually barren, with a relatively small number of species (on the latter point compare section D5).

But it must be recalled that we have discussed only the processes of obvious importance in control. We have neglected the alternative explanation of these periodicities, namely that the regular fluctuations, or some of them, may be caused or regulated largely by climatic periodicities, as suggested by Elton and others. The problem of assessing the relative importance of these two types of causes of periodicity is beyond the scope of this discussion.

What we can conclude here is that there is a general tendency to population fluctuations which would tend to be regular in a sufficiently regular environment. This arises, like control itself, from other sources besides the enemy-prey interactions of the mathematical theories. They are different in origin from the irregular fluctuations commonly arising directly or indirectly from the vagaries of the weather and from other sources, but of course the two types of variation merge together.

D5. Reduced variability in complex ecosystems

Voûte (1946) has brought together a great deal of evidence, chiefly from the literature on European forest entomology, in support of the conclusion that outbreaks of forest insect pests are more common in homogeneous woods than in mixed forests. He discusses the reasons for this in terms of his own views on control. Planted woods and some natural forests consist predominantly of one or a few species of tree, with, correspondingly, an undergrowth poor in species, and a relatively poor variety of phytophagous insects. The result is a reduction in the birds and other general predators. This 'faunistic impoverishment' tends to allow outbreaks of insect pests. On the other hand, in mixed virgin forests, particularly in the tropics, the great variety of plants supports a

considerable number of species of phytophagous insects, which form a manifold and dependable food supply upon which a relatively large number of general predators can maintain themselves. The presence of these adaptable enemies tends to prevent outbreaks of pests. Woods in which the trees are mostly of the same age are said to be particularly prone to the development of insect outbreaks, because they tend to reach a stage of maturity at which the leaves are wilting and especially susceptible, all at about the same time.

Graham (1939) also put forward the generalization that certain types of insect outbreaks principally occur in woods where one species of tree predominates.

Similarly, Engel (1942), whose observations on *Bupalus piniarius* were mentioned earlier, concluded that the enemies of this moth are normally less numerous in pure stands of the host tree than in mixed (multi-specific) stands, because no alternative hosts are available to them in the pure stands. Hence *Bupalus* can increase rapidly and reach high densities in the pure stands before being controlled by the enemies. But when the turning-point is reached, the subsequent decline is more rapid than in the mixed stands.

Again, on the basis of observations in eastern Sumatra, Schneider (1939) considered that in the natural forest each species of plant is attacked by a complex of insects, each of which is controlled by polyphagous enemies; but if a species of plant is grown in pure culture, only a few insect species and their enemies can live on it; such a biocoen is more labile than a natural one, and serious outbreaks of phytophagous species occur.

In a broad way, there is a geographical zonation of degrees of ecological complexity. The fact that terrestrial life tends to be less abundant and varied as one moves from tropical forest to temperate regions and thence to polar and other barren regions is widely recognized. Combining this point with that of the preceding paragraphs, we should expect a corresponding trend from smaller to greater variability in the densities of populations. There is evidence to support this conclusion. For example, one of the generalizations made by Graham (1939) was that periodic outbreaks of forest insects are more common in temperate than in tropical forests. Periodic fluctuations of populations are most common and marked towards the arctic regions; they are perhaps least evident in tropical forests, but this point seems to have been little studied. A suggestion well in line with this is that a characteristic of the far northern areas which leads to periodic fluctuations in the numbers of animals is their barrenness, their easily exhaustible food resources (Huntington, 1931).

It should be noted that there is a general tendency for population densities of most species in the tropical forests to be relatively low, perhaps as the result of a more intense struggle against enemies and competitors (Hesse *et al.* 1937, ch. 20). The lower density would mean smaller and less noticeable fluctuations in an absolute sense; but the proportional fluctuations are probably also smaller, because of the greater complexity of the biocoens. Another characteristic of tropical populations noted by Hesse *et al.* is that successive generations follow each other in more rapid succession in the warmer climate, and the different developmental stages commonly occur simultaneously. To whatever extent these circumstances make for reduced variability, as suggested by Bremer (1929), they must be added to the other forces opposing large fluctuations of tropical forest populations.

Of course, all this must be interpreted very flexibly and generally, and other factors besides biotic complexity should be considered, especially differences in the variability of climates. Voûte (1946) attached some importance to the idea that an irregular climate might disturb the 'balance' of a population sufficiently to lead to an outbreak.

Other aspects of the physical environment may also have an important influence on the variability of populations. For example, in a very heterogeneous physical environment, there is more likely to be a continual supply of favourable micro-habitats, however changeable the general conditions may be; on the other hand, only a certain fraction of such an environment is likely to be favourable at any one time; these circumstances would be likely to operate against any tendency to extreme variation in the density of a population. The indirect results of physical heterogeneity are likely to be more important than any direct effects. For example, patchiness in the distribution of plants, and hence also of many animals, is to a considerable extent a reflexion of differences in the soil, water supply, etc.

As Thompson (1929*c*) pointed out, the relative importance of physical to biotic factors is greatest in the barren places of the earth, and least in places like the tropical forests, where physical conditions tend to be uniformly favourable and life most abundant.

To sum up, there is considerable evidence that in the more complex biocoens, i.e. those with the greater numbers of interacting species, the variability of the populations tends to be less pronounced. A complex biocoen has many resources for compensatory action. The natural control of a population within it is many-sided, resilient and unlikely to break down. Since a varied physical environment is also likely to damp down population fluctuations, and since physical variety tends to be reflected in the plant cover and the dependent animals, the above conclusion should not be restricted to the biocoen. In short, population

variability tends to be inversely related to the degree of complexity of the ecosystem.

E. SUMMARY

A. This paper attempts to clarify the subject by giving a systematic account of the processes considered to be involved in the natural control of animal populations.

B. First, a brief survey is made of the chief types of theories offering an explanation of natural control. The earlier theories looked to natural enemies as the main agents of control. Somewhat later theories gave predominance to physical factors. Control has been attributed exclusively to competition, including competition between natural enemies, or, more broadly, to density-dependent mortality. Among theories of periodic fluctuations, many ascribe control to some aspect of overpopulation of the environment, while mathematical theories envisage control due primarily to natural enemies. Certain 'comprehensive' theories lay emphasis on the complexity and essential interconnectedness of the population-environment system, and hold that the particular causes of control vary with the circumstances.

C. The elements of natural control are outlined as follows:

C1. The numerical variation of populations is often considerable and yet is kept within certain limits.

C2. A population and the items of its environment form a closely interconnected complex or ecosystem. The relationships of a population are with the whole ecosystem (which includes itself) rather than with the environment only.

C3. The distinction between density-dependent and density-independent action is discussed, with examples; it by no means corresponds to the division between biotic and physical factors. Density-dependent action is defined as that which intensifies (per individual) as population density increases, and relaxes as density falls; it is the chief agent of control. Some processes are inversely related to density.

Control of a population is a result of the limited capacity of the ecosytem with respect to that species or with respect to its enemies or both. The limiting influence begins to operate at densities far below the capacity limit, intensifying as this limit is approached; this is the basis of most kinds of density dependence (the other kinds are modifications of environmental capacity, the degree of modification naturally depending on density). An enemy is density-dependent in its action on a host (or prey) population if it attacks a greater proportion as the host density increases. The enemy will do this if it is capable, and if the supply of the host is a limiting factor in the enemy's environment.

The presence of competitor species, and sometimes that of alternative hosts or prey for the enemies of a population, tends to intensify the action of the control factors involved.

C4. Four phases of control are distinguished: *limitation*, which sets a variable upper limit; *conservation*, which tends to prevent extreme reduction; *suppression*, or a forced decline from high density; and *release*, a temporary escape from normal control after a severe reduction. Each is brought about by characteristic density relationships. Suppression and release promote fluctuations.

C5. The level of abundance depends ultimately on all the major elements of the ecosystem, although the density-related, controlling factors are the immediate determinants. Only in regard to particular types of situations, or of animals, can more precise statements be made.

D. Some related matters are also discussed:

D1. The possibility that either physical or biotic factors may be primarily responsible for control in general is examined. Decisions can be reached only about particular types of situations.

D2. Some of the ways in which the term 'balance' or 'equilibrium' has been applied to population relationships are checked against its physical meaning. It is generally inappropriate to any except nearly constant populations, and this applies equally to 'dynamic equilibrium'. To prevent confusion, the above terms should not be used in biology without full explanation of the meaning intended.

D3. Although population variation is restricted, the view that density generally fluctuates about a mean value, and the related idea that deviations from this mean set up a tendency to return to it, are over-simplifications. The idea that density tends towards a *varying* level raises the practical difficulty of distinguishing the two sets of variations, but may be useful.

D4. The laboratory demonstration of the 'classical' oscillations predicted by the mathematical theories has so far proved very difficult. Instead, 'relaxation oscillations', in which the predator population kills all the prey and then dies out, have tended to appear. When 'refuges' are available, as in nature, remnants of each population normally survive such crashes, and may increase again. In very regular environments, a succession of these cycles might be maintained; in more general terms, a repeated cycle of suppression and release (see C4) might occur. But this is speculative, and perhaps other causes are more important in producing periodic cycles in nature.

D5. There is evidence that animal populations fluctuate less violently in very complex ecosystems, for example in tropical forests, than in woods poorer in plant and animal species, and that the most violent fluctuations tend to occur among the animals in plantations of one species, or in barren places like the

far north. Also, irregularities in the physical environment (but not in climate), by increasing the complexity of the ecosystem, probably reduce the numerical variability of populations.

F. ACKNOWLEDGEMENTS

The theoretical work from which this paper arose was undertaken as a background study to problems arising in work on pests of stored products, at the Pest Infestation Laboratory of the Department of Scientific and Industrial Research. The paper is published by permission of the Department.

It is a pleasure to thank Prof. Thomas Park, of Chicago, and Mr Charles Elton, for their critical comments on the manuscript, and Mr F. N. Ratcliffe, of the Council for Scientific and Industrial Research, Australia, for his kindness in making a detailed critique which greatly assisted revision. Particularly since I have not always followed their suggestions, it is necessary to add that they are not to be held responsible for anything in the final paper.

A discussion of this type owes more than usual to the writings of other biologists. I am glad to acknowledge this, and also my indebtedness to many colleagues for helpful discussions.

G. REFERENCES

Ahmad, T. & Ullah, G. (1939). 'Ecological studies on the spotted bollworms of cotton and their parasites. 1. The pre-imaginal development and viability of *Earias fabia* and *Microbracon lefroyi* under different conditions of temperature and humidity.' Indian J. Ent. 1: 18–47.

Alexander, W. B. (1946). 'The index of heron population, 1945.' Brit. Birds, 39: 201–6. (Including Suppl. by D. Lack.)

Allee, W. C. (1931). 'Animal aggregations: a study in general sociology.' Chicago.

Allee, W. C. (1934*a*). 'Concerning the organization of marine coastal communities.' Ecol. Monogr. 4: 541–54.

Allee, W. C. (1934*b*). 'Recent studies in mass physiology.' Biol. Rev. 9: 1–48.

Allee, W. C. (1941). 'Integration of problems concerning protozoan populations with those of general biology.' Amer. Nat. 75: 473–87 (also in Biol. Symposia, 4: 75–89, 1941).

Allee, W. C. & Park, T. (1939). 'Concerning ecological principles.' Science, 89: 166–9.

Anon. (1946). New Zealand Dep. Sci. Indust. Res. 20th Ann. Rep. p. 47.

Baker, W. A. & Jones, L. G. (1934). 'Studies of *Exeristes roborator* (Fab.), a parasite of the European corn borer, in the Lake Erie area.' Tech. Bull. U.S. Dep. Agric. No. 460: 26 pp.

Ball, E. D., Reeves, J. A., Boyden, B. L. & Stone, W. E. (1935). 'Biological and ecological factors in the control of the celery leaf tier in Florida.' Tech. Bull. U.S. Dep. Agric. No. 463: 55 pp.

Barnes, H. F. (1935). 'Studies of fluctuations in insect populations. V. The leaf-curling pear midge, *Dasyneura pyri* (Cecidomyidae).' J. Anim. Ecol. 4: 244–53.

Barnes, H. F. (1940). 'Fluctuations in insect numbers.' VI. Congr. Int. Ent., Madrid, 1935, 1: 181–6.

Beauchamp, R. S. A. & Ullyett, P. (1932). 'Competitive relationships between certain species of freshwater triclads.' J. Ecol. 20: 200–8.

Bess, H. A. (1945). 'A measure of the influence of natural mortality factors on insect survival.' Ann. Ent. Soc. Amer. 38: 472–81.

Bodenheimer, F. S. (1928). 'Welche Factoren regulieren die Individuenzahl einer Insektenart in die Natur?' Biol. Zbl. 48: 714–39.

Bodenheimer, F. S. (1930). 'Über die Grundlagen einer allgemeinen Epidemiologie der Insektenkalamitäten.' Z. Angew. Ent. 16: 433–50.

Bodenheimer, F. S. (1931). 'Der Massenwechsel in der Tierwelt. Grundriss einer allgemeinen tierischen Bevölkerungslehre.' Arch. Zool. (Ital.), Napoli, 16: 98–111.

Bodenheimer, F. S. (1938). 'Problems of animal ecology.' London.

Boyce, J. M. (1946). 'The influence of fecundity and egg mortality on the population growth of *Tribolium confusum* Duval.' Ecology, 27: 290–302.

Bremer, H. (1929). 'Grundsätzliches über den Massenwechsel von Insekten.' Z. Angew. Ent. 14: 254–72.

Carpenter, J. R. (1939). 'The biome.' Amer. Midl. Nat. 21: 75–91.

Chapman, R. N. (1928). 'The quantitative analysis of environmental factors.' Ecology, 9: 111–22.

Chapman, R. N. (1931). 'Animal ecology, with especial reference to insects.' New York, etc.

Chapman, R. N. (1933). 'The causes of fluctuations of populations of insects.' Proc. Hawaii. Ent. Soc. 8: 279–92.

Chapman, R. N. & Baird, L. (1934). 'The biotic constants of *Tribolium confusum* Duval.' J. Exp. Zool. 68: 293–304.

Chapman, R. N. & Whang, W. Y. (1934). 'An experimental analysis of the cause of population fluctuations.' Science, 80: 297–8.

Clark, C. A. (1934). 'The European corn borer and its controlling factors in the Orient.' Tech. Bull. U.S. Dep. Agric. No. 455: 37 pp.

Clarke, C. H. D. (1936). 'Fluctuations in numbers of ruffed grouse, *Bonasa umbellus* (Linne).' Univ. Toronto Stud., Biol. Ser. No. 41: 118 pp.

Clements, F. E. & Shelford, V. E. (1939). 'Bio-ecology.' New York, etc.

Cook, W. C. (1925). 'The distribution of the alfalfa Weevil (*Phytonomus posticus* Gyll.). A study in physical ecology.' J. Agric. Res. 30: 479–91.

Criddle, N. (1930). 'Some natural factors governing the fluctuations of grouse in Manitoba.' Canad. Field-Nat. 44: 77–80.

Crombie, A. C. (1943). 'The effect of crowding upon the natality of grain-infesting insects.' Proc. Zool. Soc., Ser. A, 113: 77–98.

Crombie, A. C. (1945). 'On competition between different species of graminivorous insects.' Proc. Roy. Soc. B, 132: 362–95.

Crombie, A. C. (1946). 'Further experiments on insect competition.' Proc. Roy. Soc. B, 133: 76–109.

Crombie, A. C. (1947). 'Interspecific competition.' J. Anim. Ecol. 16: 44–73.

Cutler, D. W., Crump, L. M. & Sandon, H. (1922). 'A quantitative investigation of the bacterial and protozoan population of the soil, with an account of the protozoan fauna.' Philos. Trans. B, 211: 317–50.

Darwin, C. (1859). 'On the origin of species by means of natural selection.' London.

Davidson, J. (1934). 'The "lucerne flea" *Smynthurus viridis* L. (Collembola) in Australia.' Bull. Coun. Sci. Industr. Res. Aust. No. 79: 66 pp.

De Bach, P. (1946). 'An insecticidal check method for measuring the efficacy of entomophagous insects.' J. Econ. Ent. 39: 695–7.

De Bach, P. & Smith, H. S. (1941). 'Are population oscillations inherent in the host-parasite relation?' Ecology, 22: 363–9.

De Bach, P. & Smith, H. S. (1947). 'Effects of parasite population density on rate of change of host and parasite populations.' Ecology, 28: 290–8.

Dymond, J. R. (1947). 'Fluctuations in animal populations with special reference to those of Canada.' Trans. Roy. Soc. Can. 41: 1–34.

Eckstein, F. (1939). 'Über die klimatische Bedingtheit des Zusammenbruches von Massenvermehrungen beim Maikäfer.' Verh. 7. Int. Kongr. Ent., Berlin, 1938, 3: 2190–200.

Eggleton, F. E. (1939). 'Fresh-water communities.' Amer. Midl. Nat. 21: 56–74.

Eidmann, H. (1931). 'Zur Kenntnis der Periodizität der Insektenepidemien.' Z. Angew. Ent. 18: 537–67.

Eidmann, H. (1934). 'Zur Epidemiologie der Forleule.' Mitt. Forstwirt. Forstwiss.: 13–27.

Eidmann, H. (1937). 'Zur Theorie der Bevölkerungsbewegung der Insekten.' Anz. Schädlingsk. 13: 47–52.

Elton, C. (1927). 'Animal ecology.' London.

Elton, C. (1930). 'Animal ecology and evolution.' Oxford.

Elton, C. (1942). 'Voles, mice and lemmings.' Oxford.

Engel, H. (1942). 'Über die Populationsbewegung des Kiefernspanners (*Bupalus piniarius* L.) in verschiedenen Bestandstypen.' Z. Angew. Ent. 29: 116–63.

Errington, P. L. (1945). 'Some contributions of a fifteen-year local study of the northern bobwhite to a knowledge of population phenomena.' Ecol. Monogr. 15: 1–34.

Errington, P. L. (1946). 'Predation and vertebrate populations.' Quart. Rev. Biol. 21: 144–77, 221–45.

Escherich, K. (1914). 'Die Forstinsekten Mitteleuropas.' Vol. 1. Berlin.

Escherich, K. (1924). 'Vortrag des Professors Dr Escherich in Münnchen. [Kieferneulenkatastrophe und Forstentomologie.].' Ber. Hauptversammlung Deutsch. Forstvereins zu Bamberg 1924, 21: 147–59.

Evans, F. C. (1942). 'Studies of a small mammal population in Bagley Wood, Berkshire.' J. Anim. Ecol. 11: 182–97.

Flanders, S. E. (1935). 'Effect of host density on parasitism.' J. Econ. Ent. 28: 898–900.

Flanders, S. E. (1946). 'Control of sex and sex-limited polymorphism in the Hymenoptera.' Quart. Rev. Biol. 21: 135–43.

Flanders, S. E. (1947). 'Elements of host discovery exemplified by parasitic Hymenoptera.' Ecology, 28: 299–309.

Ford, J. (1937). 'Research on populations of *Tribolium confusum* and its bearing on ecological theory: a summary.' J. Anim. Ecol. 6: 1–14.

Friederichs, K. (1927). 'Die Bedeutung der Biocönosen für den Pflanzenschutz gegen Tiere.' Z. Angew. Ent. 12: 385–411.

Friederichs, K. *et al.* (1930). 'Die Grundfragen und Gesetzmässigkeiten der land- und forstwirtschaftlichen Zoologie, insbesondere der Entomologie.' 2 vols. Berlin.

Fuller, M. E. (1934). 'The insect inhabitants of carrion: a study in animal ecology.' Bull. Coun. Sci. Industr. Res. Aust. No. 82: 62 pp.

Gause, G. F. (1934). 'The struggle for existence.' Baltimore.

Gause, G. F. (1937). 'Experimental populations of microscopic organisms.' Ecology, 18: 173–9.

Graham, S. A. (1939). 'Forest insect populations.' Ecol. Monogr. 9: 301–10.

Green, R. G. & Evans, C. A. (1940). 'Studies on a population cycle of snowshoe hares on the Lake Alexander area....' J. Wildlife Management, 4: 220–38, 267–78, 347–58.

Green, R. G., Larson, C. L. & Bell, J. F. (1939). 'Shock disease as the cause of the periodic decimation of the snowshoe hare.' Amer. J. Hyg. 30: 83–102.

Hammond, E. C. (1938, 1939). 'Biological aspects of population density in lower organisms.' Quart. Rev. Biol. 13: 421–38 and 14: 35–59.

Hardy, J. E. (1938). '*Plutella maculipennis* Curt., its natural and biological control in England.' Bull. Ent. Res. 29: 343–72.

Hartley, P. H. T. (1947). 'Predation by sparrow-hawk populations.' Ecology, 28: 326–8. [Review of Tinbergen, L. (1946). 'De Sperwer als Roofvijand van Zangvogels.' Arde. 34: 1–213.]

Hesse, R., Allee, W. C. & Schmidt, K. P. (1937). 'Ecological animal geography.' New York, etc.

Holdaway, F. G. (1932). 'An experimental study of the growth of populations of the "flour beetle" *Tribolium confusum* Duval, as affected by atmospheric moisture.' Ecol. Monogr. 2: 261–304.

Howard, L. O. & Fiske, W. F. (1911). 'The importation into the United States of the parasites of the gipsy moth and the brown-tail moth.' Bull. U.S. Bur. Ent. No. 91: 312 pp.

Huntington, E. (1931). 'The Matamek Conference on Biological Cycles, 1931.' Science, 74: 229–35.

Hutchinson, G. E. (1941). 'Ecological aspects of succession in natural populations.' Amer. Nat. 75: 406–18.

Janisch, E. (1938). 'Untersuchungen über den Massenwechsel von Schadinsekten.' Z. PflKrankh. 48: 435–48.

Janisch, E. (1939). 'Die Bedeutung des Optimums für den Massenwechsel forstschädlicher Insekten.' Verh. 7. Int. Kongr. Ent., Berlin, 1938, 3: 1974–89.

Kalabukhov, N. I. (1935). ['On the causes of the fluctuations in numbers of mouse-like rodents.'] Zool. Zh. 14: 209–42. (In Russian; English summary.)

Lack, D. (1943). 'The life of the robin.' London.

Lindeman, R. L. (1942). 'The trophic-dynamic aspect of ecology.' Ecology, 23: 399–418.

Lotka, A. J. (1925). 'Elements of physical biology.' Baltimore.

Macfadyen, A. (1948). 'The meaning of productivity in biological systems.' J. Anim. Ecol. 17: 75–80.

McKenzie, H. L. (1943). 'The seasonal history of *Matsucoccus vexillorum* Morrison (Homoptera: Coccoidea: Margarodidae).' Microentomology, 8: 42–52.

MacLagan, D. S. (1932). 'An ecological study of the "lucerne flea" (*Smynthurus viridis*, Linn.). I & II.' Bull. Ent. Res. 23: 101–45, 151–90.

MacLagan, D. S. (1941). 'Recent animal-population studies; and their significance in relation to socio-biological philosophy (Part I).' Proc. Univ. Durham Phil. Soc. 10: 310–31.

MacLagan, D. S. & Dunn, E. (1935). 'Experimental analysis of population growth.' Nature, Lond., 135: 33–4.

MacLulich, D. A. (1937). 'Fluctuations in the numbers of the varying hare (*Lepus americanus*).' Univ. Toronto Stud., Biol. Ser. No. 43: 136 pp.

Muir, F. (1931). 'The critical point of parasitism and the Law of Malthus.' Bull. Ent. Res. 22: 249–51.

Nice, M. M. (1937). 'Studies in the life history of the song sparrow. I. A population study of the song sparrow.' Trans. Linn. Soc. N.Y. 4: 1–247.

Nicholson, A. J. (1927). 'A new theory of mimicry in insects.' Aust. Zool. 5: 10–104.

Nicholson, A. J. (1933). 'The balance of animal populations.' J. Anim. Ecol. 2: 132–78.

Nicholson, A. J. & Bailey, V. A. (1935). 'The balance of animal populations. Part 1.' Proc. Zool. Soc. Lond. 551–98.

Oxley, T. A. & Howe, R. W. (1944). 'Factors influencing the course of an insect infestation in bulk wheat.' Ann. Appl. Biol. 31: 76–80.

Park, T. (1932). 'Studies in population physiology: The relation of numbers to initial population growth in the flour beetle *Tribolium confusum* Duval.' Ecology, 13: 172–81.

Park, T. (1933). 'Studies in population physiology. II. Factors regulating initial growth of *Tribolium confusum* populations.' J. Exp. Zool. 65: 17–42.

Park, T. (1934). 'Observations on the general biology of the flour beetle, *Tribolium confusum*.' Quart. Rev. Biol. 9: 36–54.

Park, T. (1938). 'Studies in population physiology. VIII. The effect of larval population density on the post-embryonic development of the flour beetle, *Tribolium confusum* Duval.' J. Exp. Zool. 79: 51–70.

Park, T. (1941). 'The laboratory population as a test of a comprehensive ecological system.' Quart. Rev. Biol. 16: 274–93, 440–61.

Park, T. (1942). 'Integration in infra-social insect populations.' Biol. Symposia, 8: 121–38.

Park, T. (1948). 'Experimental studies of interspecies competition. I. Competition between populations of the flour beetles, *Tribolium confusum* Duval and *Tribolium castaneum* Herbst.' Ecol. Monogr. 18: 265–307.

Park, T., Gregg, E. V. & Lutherman, C. Z. (1941). 'Studies in population physiology. X. Interspecific competition in populations of granary beetles.' Physiol. Zool. 14: 395–430.

Parsons, F. S. & Ullyett, G. C. (1936). 'Investigations on *Trichogramma lutea*, Gir., as a parasite of the cotton bollworm, *Heliothis obsoleta*, Fabr.' Bull. Ent. Res. 27: 219–35.

Payne, N. M. (1934). 'The differential effect of environmental factors upon *Microbracon hebetor* Say (Hymenoptera: Braconidae) and its host, *Ephestia Kühniella* Zeller (Lepidoptera: Pyralidae). II.' Ecol. Monogr. 4: 1–46.

Pearl, R. (1926). 'The biology of population growth.' London.

Pearl, R. & Parker, S. L. (1922*a*). 'Experimental studies on the duration of life. II. Hereditary differences in duration of life in line-bred strains of *Drosophila*.' Amer. Nat. 56: 174–87.

Pearl, R. & Parker, S. L. (1922*b*). 'Experimental studies on the duration of life. IV. Data on the influence of density of population on the duration of life in *Drosophila*.' Amer. Nat. 56: 312–21.

Pruthi, H. S. (1940). 'Ecology and control of insects.' Proc. 27th Indian Sci. Congr., Sect. Entom.: 261–308. [See summary in 1939, Indian J. Ent. 1: 87–91.]

Richards, O. W. (1940). 'The biology of the small white butterfly (*Pieris rapae*), with special reference to the factors controlling its abundance.' J. Anim. Ecol. 9: 243–88.

Ross, R. (1908). 'Report on the prevention of malaria in Mauritius.' London.

Salt, G. (1932). 'The natural control of the sheep blowfly, *Lucilia sericata*, Meigen.' Bull. Ent. Res. 23: 235–45.

Salt, G. (1936). 'Experimental studies in insect parasitism IV. The effect of superparasitism on populations of *Trichogramma evanescens*.' J. Exp. Biol. 13: 363–75.

Schneider, F. (1939). 'Ein Vergleich von Urwald und Monokultur in Bezug auf ihre Gefährdung durch phytophage Insekten, auf Grund einiger Beobachtungen an der Ostküste von Sumatra.' Schweiz. Z. Forstw. 90: 41–55, 82–9.

Schwerdtfeger, F. (1934). 'Über den Verlauf von Insektengradationen. Dargestellt an einigen Forstschädlingen.' Verh. Dtsch. Ges. Angew. Ent. 9: 32–41.

Schwerdtfeger, F. (1935). 'Studien über den Massenwechsel einiger Forstschädlinge. II. Über die Populationsdichte von *Bupalus piniarius* L., *Panolis flammea* Schiff., *Dendrolimus pini* L., *Sphinx pinastri* L. und ihren zeitlichen Wechsel.' Z. Forst- u. Jagdw. 67: 449–82, 513–40.

Schwerdtfeger, F. (1941). 'Über die Ursachen des Massenwechsels der Insekten.' Z. Angew. Ent. 28: 254–303.

Severtzoff, S. A. (1934). 'On the dynamics of populations of vertebrates.' Quart. Rev. Biol. 9: 409–37.

Smith, H. S. (1929). 'Multiple parasitism: its relation to the biological control of insect pests.' Bull. Ent. Res. 20: 141–9.

Smith, H. S. (1935). 'The rôle of biotic factors in the determination of population densities.' J. Econ. Ent. 28: 873–98.

Smith, H. S. (1937). Review: Sweetman, H. L., 1936, 'The biological control of insects.' Ithaca, N.Y. J. Econ. Ent. 30: 218–20.

Smith, H. S. (1939). 'Insect populations in relation to biological control.' Ecol. Monogr. 9: 311–20.

Smith, H. S. & De Bach, P. (1942). 'The measurement of the effect of entomophagous insects on population densities of their hosts.' J. Econ. Ent. 35: 845–9.

Solomon, M. E. (1946). 'Tyroglyphid mites in stored products. Ecological studies.' Ann. Appl. Biol. 33: 82–97.

Stanley, J. (1932). 'A mathematical theory of the growth of populations of the flour beetle, *Tribolium confusum*, Duv.' Canad. J. Res. 6: 632–71.

Stanley, J. (1938). 'The egg-producing capacity of populations of *Tribolium confusum* Duv. as affected by intensive cannibalistic egg-consumption.' Canad. J. Res. 16: 300–6.

Stanley, J. (1941). 'A mathematical theory of the growth of populations of the flour beetle *Tribolium confusum* Duv. IV. A modified theory descriptive of the relation between the limiting value of egg-populations in the absence of hatching, and the volume (or weight) of flour used in the culture.' Ecology, 22: 23–37.

Tansley, A. G. (1935). 'The use and abuse of vegetational concepts and terms.' Ecology, 16: 284–307.

Taylor, T. H. C. (1937). 'The biological control of an insect in Fiji....' London.

Thompson, W. R. (1923). 'A criticism of the "sequence" theory of parasitic control.' Ann. Ent. Soc. Amer. 16: 115–28.

Thompson, W. R. (1928). 'A contribution to the study of biological control and parasitic introduction in continental areas.' Parasitology, 20: 90–112.

Thompson, W. R. (1929*a*). 'On the relative value of parasites and predators in the biological control of insect pests.' Bull. Ent. Res. 19: 343–50.

Thompson, W. R. (1929*b*). 'On the part played by parasites in the control of insects living in protected situations.' Bull. Ent. Res. 20: 457–62.

Thompson, W. R. (1929*c*). 'On natural control.' Parasitology, 21: 269–81.

Thompson, W. R. (1930). 'The biological control of insect and plant pests.' E.M.B. [Publ.], 29: 124 pp. London.

Thompson, W. R. (1939). 'Biological control and the theories of the interactions of populations.' Parasitology, 31: 299–388.

Tothill, J. D. (1922). 'The natural control of the fall webworm (*Hyphantria cunea* Drury) with an account of its several parasites.' Bull. Canad. Dep. Agric. N.S. 3 (Ent. Bull. 19): 107 pp.

Ullyett, G. C. (1936). 'The physical ecology of *Microplectron fuscipennis*, Zett. (Hym. Chalc.).' Bull. Ent. Res. 27: 195–217.

Ullyett, G. C. (1938). 'The encouragement of beneficial insects.' S. Afr. Dep. Agric. For. Bull. No. 189: 10 pp.

Ullyett, G. C. (1945). 'Distribution of progeny by *Microbracon hebetor* Say.' J. Ent. Soc. S. Afr. 8: 123–31.

Ullyett, G. C. (1947). 'Mortality factors in populations of *Plutella maculipennis* Curtis (Tineidae: Lep.), and their relation to the problem of control.' Ent. Mem. Union S. Afr. Dep. Agric. For. 2: 77–202.

Uvarov, B. P. (1931). 'Insects and climate.' Trans. Ent. Soc. Lond. 79: 1–247.

Varley, G. C. (1947). 'The natural control of population balance in the knapweed gall-fly (*Urophora jaceana*).' J. Anim. Ecol. 16: 139–87.

Volterra, V. (1926). 'Variazioni e fluttuazioni del numero d'individui in specie animali conviventi.' Mem. Accad. Lincei, ser. 6, 2 (3): 31–112. (Cf. translation in Chapman, 1931, pp. 409–48.)

Volterra, V. (1928). 'Variations and fluctuations of the number of individuals in animal species living together.' J. Cons. Int. Explor. Mer, 3 (1): 3–51. (Also given as Appendix to Chapman, R. N. (1931): 409–48.)

Volterra, V. (1931). 'Leçons sur la théorie mathématique de la lutte pour la vie.' Paris.

Voûte, A. D. (1943). 'Classification of factors influencing the natural growth of a population of insects.' Acta Biotheoretica, 7: 99–116.

Voûte, A. D. (1946). 'Regulation of the density of the insect-populations in virgin-forests and cultivated woods.' Arch. Néerl. Zool. 7: 435–70.

Williams, C. B. (1947). 'The field of research in preventive entomology.' Ann. Appl. Biol. 34: 175–85.

Williams, F. X. (1931). 'Handbook of the insects and other invertebrates of Hawaiian sugar cane fields.' Honolulu.

Wilson, F. (1946). 'Interaction of insect infestation, temperature, and moisture content in bulk-depot wheat.' Bull. Coun. Sci. Industr. Res. Aust. No. 209: 31 pp.

Zwölfer, W. (1930). 'Zur theorie der Insektenepidemien.' Biol. Zbl. 50: 724–59.

Zwölfer, W. (1935). 'Die Temperaturabhängigkeit der Entwicklung der Nonne (*Lymantria monacha* L.) und ihre bevölkerungswissenschaftliche Auswertung.' Z. Angew. Ent. 21: 333–84.

ADDENDUM

Among the papers I had not seen when this discussion was written, one of special importance is Ullyett's treatise (1947). Special attention is paid to the density-dependence of the mortality factors. There is a rather full discussion of general principles bearing on the natural control of *Plutella*, with some interesting conclusions about artificial control measures.

SURFACE FILMS ON NATURAL BODIES OF WATER

By R. J. GOLDACRE

The Chester Beatty Research Institute, The Royal Cancer Hospital, London, S.W. 3

1. GENERAL

The behaviour of particles of dust on the surface of ponds and rivers under the action of currents in the air or the water suggests that their movement is controlled by an elastic film at the air-water interface. As adventitious films occur in the laboratory in work on monomolecular layers and must be swept off before an experiment can be begun, it is of interest to determine whether on natural bodies of water such films exist, and if so to what extent. The presence of films on sea water and on some rivers has been demonstrated by Adam (1937). In what follows the observations are extended and the possible ecological significance of the films is discussed.

Surface films were detected on practically every natural body of water investigated in various parts of England. The surface pressure (F) in dynes per cm. of the film *in situ* was measured by the use of a series of oils of graded spreading pressures. A drop of each oil was placed on the surface, starting with the oil with least tendency to spread, until one was found which expanded against the surface pressure of the film present. This gave the limits within which the pressure lay. The oils used were tricresylphosphate, castor oil, oleic acid and indicator oils prepared by the method of Langmuir and Schaeffer (1939), to show colour changes in the range $F = 2–5$ and $F = 4–15$, and calibrated on the Langmuir surface-balance. The expansion of the oil was indicated by the movement of particles of dust resting on the film, or in the case of the indicator oils by the appearance of the interference colour corresponding to the pressure at that point. Where the pressure was too low to be measured with the oil available (as with many of the films in the range $F = 0–2$) films were detected by placing a second indicator oil-drop next to the first. On expanding it did not run into the first, but pushed it when its edge was still several millimetres away, showing that there was an invisible film between them.

In some cases the oil expanded in an irregular, star-shaped pattern, indicating that the film was solid. Such cases are marked (S) in Table 1.

The results are grouped according to the surface pressures found. For comparison, the pressures on some artificial bodies of water are included. It must be noted that the values apply only at the time of measurement, owing to the influence of the weather. The observations were made in the autumn and early winter of 1946. Table 1 shows the distribution of the films.

In general, the lowest pressures were found in rivers and streams, and the highest in stagnant ponds and lakes. The reason for this can easily be observed. Moving water is constantly being swept by the wind and by floating barriers, and the film is collected in pockets between rocks, sticks and leaves at the sides, and swirls in the water keep pushing the film against the side, where it collapses. Measurements of F at the side of a river were often above 30, whereas at the same time in the centre of the river F was less than 2 dynes/cm. Frequently a stream flows under a stationary floating branch which is holding debris such as smaller sticks and floating leaves pressed together on the surface. Any leaks soon become filled with film which usually solidifies as the pressure increases and so the leaks are sealed. Film accumulates at such a barrier when it is brought down at a rate faster than it can flow back under the influence of the surface-pressure gradient. Measurement usually shows that F on the downstream side is close to zero, and on the upstream side diminishes from above 30 at the barrier to near zero a few dozen yards farther upstream. The surface pressure is usually high (> 15) in any froth. Care was taken not to make measurements near any obvious contamination, or on windy days.

The wind has a very big effect on F. A rough estimate was obtained by placing drops of indicator oil at intervals along a 6 ft. diameter pool on which a film (with $F = 3$) was present. The oil-drops expanded to the same size and colour, showing that the film was uniform. A breeze of about 6 m.p.h. at head level rose and caused changes in the colour and size of the drops, which, however, returned to their original condition when the wind dropped. The change in F in the direction of the wind was about 1 dyne/cm./ft. Since each part of the film presses on the part next to it in the direction of the wind, the wind-induced pressure is proportional to the length of film over which the wind has blown. Thus such a wind blowing over a 100 ft. lake would produce a surface pressure at the edge of 100 dynes/cm., sufficient to collapse any film. Such collapsed films can usually be observed on the side of lakes towards which the wind is blowing, in the form of myriads of tiny fibres parallel to the

Table 1

F = 0–2 dynes/cm.

Lake at Balcome
R. Ouse at Lewes
Pond at Hampstead Heath
Pond at Highgate
Dover Canal
R. Cam above Cambridge and at King's College
Rydal Water (Cumberland)
Stream at Grasmere (*S*)
Lake Grasmere (not near stream mouths)
Pool near Elterwater (*S*)
Great Langdale Beck
Derwent Water
River at Keswick
River at Patterdale
Grisdale Tarn (2000 ft.)
R. Lune at Kirkby Lonsdale (*S*)—higher values also recorded, between rocks, v.i.
R. Ribble at Settle
Stream near Hayfield
Stream near Cat and Fiddle (Derbyshire)
Stream at Llangollen
River at Chirk
Canal at Preesgweene
R. Severn at Shrewsbury
Stream near Pen-y-Stryt

F = 2–5 dynes/cm.

Serpentine Lake
Ponds at Hampstead Heath
Lake Grasmere at junction with stream (*S*)
Stream at Grasmere
Stream near Buxton (*S*)
R. Severn at Montford (*S*)
R. Avon at Stratford (*S*)

F = 5–10 dynes/cm.

Pond at Regent's Park
Pond at Shottery
Grassy swamp near Pen-y-Stryt
Lake at Compton Verney
Serpentine Lake—behind leaf barrier
R. Avon, 2 miles above Stratford

F = 10–20 dynes/cm.

Pond at Crawley (*S*)
Lake at Brighton (in Park)
Pond at Lewes
Lake in St James's Park (London) (*S*)
Pond at Reigate Castle (*S*)
Pond at Highgate (swimming pool)
Grasmere lake at junction with stream (*S*)
Pond at Holmes Chapel
Pond at Chelford
Pocket at side of stream near Buxton

F = 20–30 dynes/cm.

Lake at Hampstead Heath where stream enters
Canal at Lewes
Grand Union Canal at Regent's Park
Pond in Vale of Health, Hampstead Heath
Puddle in Hyde Park (*S*)

F > 30 dynes/cm.

Pond at Brighton
Lake in St James's Park (*S*)
Pond in Trafalgar Square
Ditch near Cambridge
Puddle in field near Much Wenlock
R. Avon in collapsed film at side, at Stratford
Stream at Llangollen, in collapsed film above a floating barrier
R. Lune at Kirkby Lonsdale, between rocks towards which eddies kept bringing film

shore ('scum'). In such material oleic acid will not spread unless the wind has stopped blowing, when the material is cracked apart by the oil.

It is not to be expected, therefore, that a film could ever cover the whole of a large lake, or sea, for the slightest breeze would blow it to one side and cause it to collapse.

The flow of either the air or the water may cause concentration of the film. Thus, a stream with $F = 2$ running into Lake Grasmere caused the pressure to rise to $F = 15$ at the point of entry, whereas a hundred yards away and at most other parts of the lake F was less than 2.

2. ORIGIN AND NATURE OF THE FILM

The films are probably derived from decomposing plant tissue and (except on canals) almost certainly not due to man-made contamination. In all cases the natural water (i.e. excluding canals and artificial pools) supported abundant plant, and sometimes animal, life. The films did not have the properties of lubricating oil, for in many cases they were solid, and could be collapsed into fibres, which oil will not do. The indicator-oil expansion patterns often showed coloured fringes, which Langmuir and Waugh (1940) have shown can be caused by protein in solution.

Some freshly fallen autumn leaves were just covered in water and soaked for 3 days, and the straw-coloured filtrate placed in a trough, swept clean, and the surface pressure measured at intervals. It rose from zero at the rate of 1½ dynes/cm./min. up to over 30 dynes/cm. (a dilute—(0·01 %)—solution of gelatin behaved similarly). This shows that solution of plant material would be adequate to explain the films observed. Further, almost everything pushed through the surface of water shed a film, including fresh leaves, even those of wheat grown under a bell

jar so as to avoid gross atmospheric contamination. Soil, mould spores, carrot tissue, wheat rootlets grown in an inorganic culture medium, all readily shed films when touched to the surface of water. The films were detected by indicator oil, which was pushed back.

The films can arise either from material falling on the surface from the air (spores, soot, etc.) or from material in solution. It is probable that in most cases the films are mainly protein or lipo-protein, in view of the presence of these materials in the plants and animals in the water and in the soil around it, and also because the mechanical properties (extensibility, plasticity) of the fibres formed from the collapsed films were found to be similar to those of fibres formed in the laboratory from collapsed monolayers of protein and lipo-protein, but dissimilar to those from most other spreading substances tried, which gave much more brittle fibres or collapse structures which could not be handled mechanically.

3. SIGNIFICANCE OF FILMS

The presence of films explains why oil used to control malaria-carrying mosquitoes sometimes does not spread effectively on the water, especially on swamps where there is much decaying vegetable material. In such places the pressure of the film already present is often too high to allow the extensive expansion of an oil film.

It may be a biological advantage for some surface-growing plants to grow where the film is solid and the film pressure is high, so that they are held in position and do not pile against one another or drift against the shore. When the wind blows they move towards the shore as the film is compressed, and when the wind drops the re-expansion of the film moves them out again.

The surface film is grasped by small animals when they move about. It provides reaction by means of which small hopping arthropods can jump sideways on the water surface. (The thin layer of water which moves with the film in the hydrodynamical boundary layer (Crisp, 1946) provides a mass of material to be pushed backwards, which is comparable with the mass of the animal.) Certain fresh-water snails crawl upside down along the under-surface of the water. That they are grasping the film is shown by their being displaced when the film is pushed sideways without moving the water (for example by expanding a drop of oil nearby, or by moving a floating wooden rod slowly some distance away). Tests with oil in these places usually show that the film has a high surface pressure ($F > 10$) and is fairly rigid.

In the absence of a film of any rigidity there would be nothing to prevent a particle in the surface from being moved sideways under the smallest force, such as a current of air. The behaviour of surface-skating and clinging animals on a perfectly clean water surface hardly arises, however, since they would inevitably shed a monolayer from the material of their own bodies. For the sake of economy they may prefer to go where there is already a surface film, or to a small rather than a large water surface so that it can easily be covered with film.

The microscope revealed large numbers of small organisms entangled in film scraped from the water surface of lakes. The film may provide a source of food for small organisms, and in a much higher concentration than in the bulk of the solution. The spread 'denatured' proteins would also be more readily attached chemically than those in the solution (Neurath, Greenstein, Putnam & Erickson, 1944).

An aquarium containing soil and aquatic plants and animals maintained a film pressure of between 10 and 20 dynes/cm. even though the film was periodically swept off. The film was evidently replenished from the plant and animal material in the water. Tadpoles kept in the aquarium were often observed to turn upside down at the surface and eat the film. From the motion of dust particles towards a tadpole's mouth it was estimated that the film was being eaten at the rate of about $\frac{1}{2}$ sq.cm./sec. At this rate in one day a tadpole could consume an amount of protein monolayer equal to its own dry weight. The film could thus contribute a significant proportion of the diet, apart from the micro-organisms entangled in the film and eaten with it. Alternatively, it would provide a convenient vehicle for drawing the organisms into the tadpole's mouth.

A film collapsed by the wind consists of hollow fibres of about the diameter of plant cells. These hollow fibres which enclose the solution underneath them must be formed in myriads every day all over the world in great variety. It seems not improbable that such structures may have played a part in the evolution of the cell.

4. SUMMARY

Surface films have been found on practically all natural water surfaces which have so far been tested in various parts of England. In most cases they are monomolecular and made of protein or lipo-protein. The distribution of the two-dimensional surface pressure of the film on flowing water is indicated, and natural features causing very high surface pressures and collapse of the film are described. The ecological significance of the film is discussed, including the use of it made by some small organisms for locomotion and food.

REFERENCES

Adam, N. K. (1937). 'A rapid method for determining the lowering of tension of exposed water surfaces, with some observations on the surface tension of the sea and of inland waters.' Proc. Roy. Soc. B, 122: 134–9.

Crisp, D. J. (1946). 'Two-dimensional transport at fluid interfaces.' Trans. Faraday Soc. 42: 619–35.

Langmuir I. & Schaeffer, U. J. (1939). 'Properties and structure of protein monolayers.' Chem. Rev. 24: 181.

Langmuir, I. & Waugh, D. F. (1940). 'Pressure-soluble and pressure-displaceable components of monolayers of native and denatured proteins.' J. Amer. Chem. Soc. 62: 2771–93.

Neurath, H., Greenstein, J. P., Putnam, F. W. & Erickson, J. O. (1944). 'The chemistry of protein denaturation.' Chem. Rev. 34: 157–65.

THE NEWFOUNDLAND SEAL FISHERY AND THE SECOND WORLD WAR

By J. S. COLMAN

(With 7 Figures in the Text)

The two main activities of the Newfoundlanders are the cod-fishery in summer and autumn, and logging for the newsprint industry in the winter; in between comes the annual seal hunt which lasts for a month or six weeks in March and April. This has not been a very large fishery, in the years before the second World War employing only about 1300 men. 120 years ago, however, 10,000 men went annually on the seal hunt, and in the years before 1914 the crews still numbered between 3000 and 4000. Its importance to Newfoundland, however, is not to be measured by its absolute size. Newfoundland in normal times is a poor country, and the seal fishery can be reckoned to bring in some $300,000 a year, of which one-third is divided among the members of the crews. Furthermore, this sum comes in just when it will do most good, when the men are fitting themselves out for the summer cod-fishery. Another point worth remembering is that the seal hunt excites the whole island, and is a very welcome fillip to life towards the end of the long and savage winter; Newfoundland would lose a good deal psychologically if the seal hunt were to be discontinued.

In a former paper (Colman, 1937) the fishery was reviewed up to the year 1936, mainly with a view to determining whether or not the seals were being overfished; it was concluded that at the then rate of fishing the seals were holding their own or even increasing, but that overfishing does take place whenever the number of sealers approaches 4000. This happy state of affairs (happy from the seals' point of view, that is) seems to have been largely due to the halving of the fleet of sealing steamers during the first World War. In 1936 it seemed as though the fishery would continue for some time at its then level; no new ships were being introduced, but sealing steamers are stout craft, and most of them seemed good for perhaps another 10 or 20 years. The second World War, however, practically finished off what was left of the fleet, and at the present time the aged *Eagle* and the *Sable Island* seem to be the only sealing steamers left.

In 1943, for the first time in at least 150 years, there was no 'spring' seal fishery. One ship went out in 1944 and had a reasonably successful trip, and then in 1945 a completely new phase started with the use of motor-vessels of about 100 tons. This new fleet has increased rapidly, until in 1947 a total of 17 vessels (only two of them steamers) pursued the fishery with a total tonnage of 2276. (By way of contrast, the 20 vessels in 1914 had a tonnage of 12,067.) In this development there are several new and encouraging features, but before considering the post-war phase in detail, and in order to place it in its proper perspective, the history and nature of the Newfoundland seal fishery must first be briefly reviewed.

Two species of seal are hunted, the saddleback, Greenland or harp seal (*Phoca groenlandica*), and the bladdernose or hood seal (*Cystophora cristata*); these are always called 'harps' and 'hoods' respectively in Newfoundland. The prime object of the hunt is the baby harps or 'whitecoats' during their first 3 weeks after birth; at this stage they not only lie helpless on the ice and are easily killed, but are covered with a valuable coat of white wool. The adults of both species are hairy and their hides are of much less value, the seals, both young and old, being hunted primarily for their oil. This is of better quality and, weight for weight, more abundant in the young of both species; the young hoods, however, are harder to catch than the young harps, being able to swim almost from birth, and they do not possess the valuable white coat. Harps of all ages make up about nine-tenths of the total catch.

The seals of both species first approach the Newfoundland region from the north, swimming down the Labrador coast in November. At the Straits of Belle Isle (see map, Fig. 1) some turn into the Gulf of St Lawrence, but most proceed down the east coast. Eventually they congregate on the banks south of Newfoundland during January and February, feeding voraciously on cod and becoming very fat; during the breeding season which follows, they hardly eat at all. Many observers (see Chafe, 1923) have commented on the close discipline of these migrating hordes. The harps hug the shore in long strings of seals, while the hoods move in equally compact companies a few miles out to sea. In between come the immature seals of both species; these are less than 5 years old, and are locally called 'bedlamers', a corruption of 'bêtes de la mer'. The bedlamers of both species together form a disorderly rabble between the disciplined ranks of their elders, and it is hard to see why these non-breeding seals should accompany the breeding migration in this way.

In February the seals leave the banks and make for

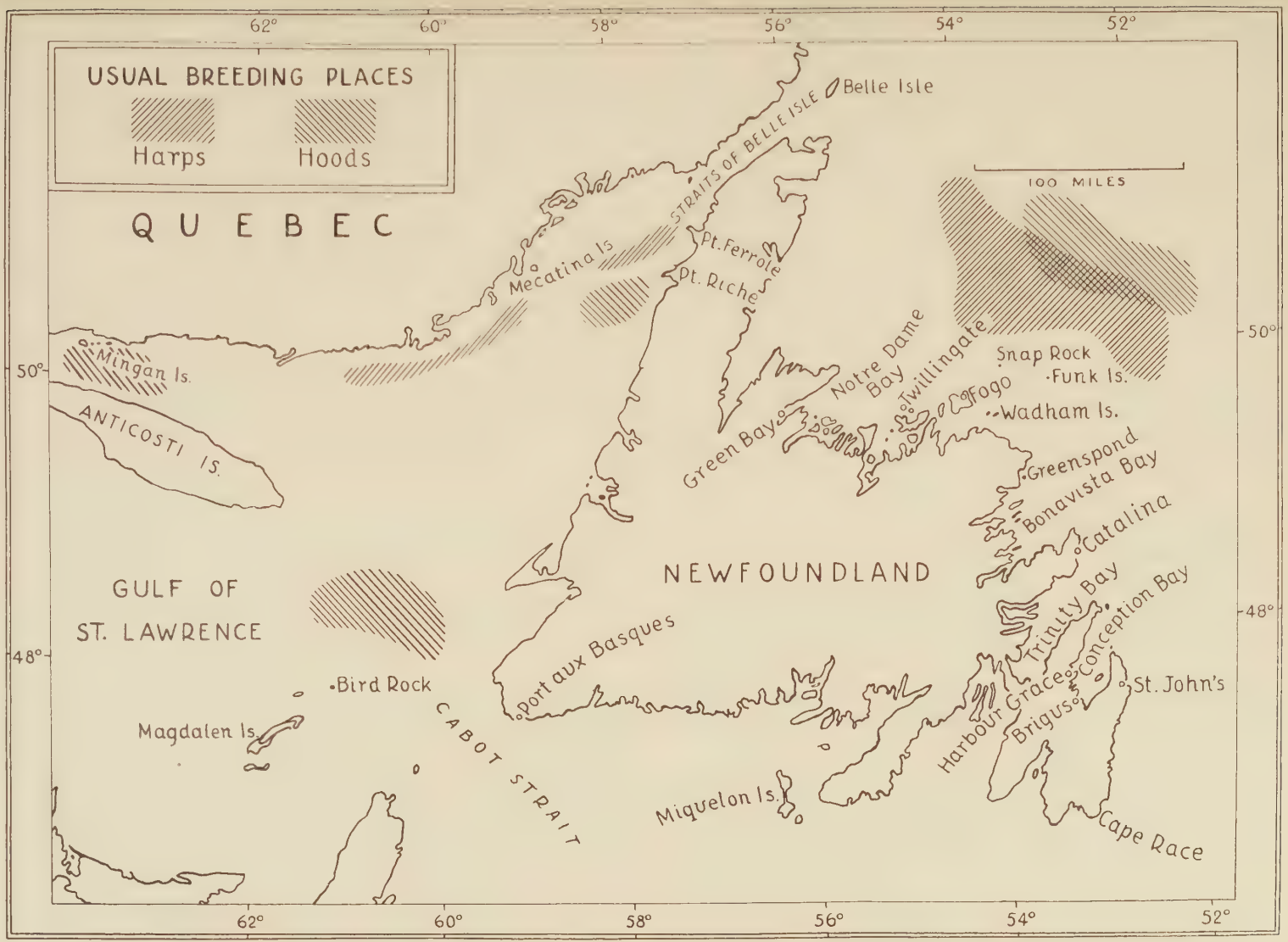


Fig. 1. Map, showing the usual breeding areas in the Newfoundland region of the harps (*Phoca groenlandica*) and the hoods (*Cystophora cristata*), and some of the main sealing ports.

the edge of the sea-ice on which they are to bring forth their young. Once again, while some go back through Cabot Strait to the Gulf of St Lawrence, the majority go up the east coast, to Notre Dame Bay, and usually find the ice somewhere off the Funk Islands. The position of the edge of this ice-field is governed largely by the wind; in some seasons it may be driven so far to the west that the breeding grounds are within sight of the shore, whereas on other occasions the seals congregate as much as 60 or a 100 miles to seaward of the Funk Islands. The breeding grounds in the Gulf are similarly variable, and are more scattered. The harps usually form two patches, one off Point Ferrole and the other strung along the shore to the westward of the Mecatina Islands; the hoods usually have one breeding ground north of Bird Rock, and another one either south-west of Point Riche, or round the Mingan Islands between Anticosti and the Quebec mainland. Oddly enough, whereas off the Funk Islands the hoods take up their position some 30 miles north and east of the harps in the Gulf the two species do not remain such close neighbours and the hoods tend to lie south and west of the harps. According to Chafe (1923), some sealers are of the opinion that the Gulf harps constitute a separate race, being shorter and thicker than those off the Funk Islands. The areas within which the breeding grounds of both species are most commonly found are shown in the map.

The ships have to find the seals in the second week in March, which is more likely to bring gales, snow and fog than any other kind of weather. The consequent difficulty of finding the breeding herds makes the fishery something of a gamble from year to year, and this is one of the reasons why this exceptionally tough and rugged hunt is so popular among the Newfoundlanders. The hunting technique has not altered in any important way for 150 years. The ships are brought through the ice as near the seals as they can get, whereupon the crews take to the ice and go among the seals with clubs called 'sealing bats', slaughtering every seal they can reach. This, of course, involves chiefly the baby seals and their mothers, and it is most surprising that the seal population has been able to withstand this sort of attack as well as it has. The harps start pupping about 1 March, and the pups take to the water in 3 weeks or so; the legal date for killing is now 10 March, but has been varied from time to time by legislation.

Soon after the breeding season the harps moult, and during May they disappear in a northerly direction; they are not seen again until they approach the Labrador coast the following November. The hoods do not moult until June or July, and the Newfoundland hoods are believed to form part of the large population that rides the ice for this purpose in the Denmark Strait between Iceland and Greenland (see Nansen, 1925). The moulting harps, though they spend much of their time on the ice off the Funks, are not hunted intensively by the Newfoundlanders; they are by then thin, and their pelts produce relatively little oil.

In the sixteenth, seventeenth and eighteenth centuries seals were caught by Breton, Basque and Jersey fishermen around the Straits of Belle Isle, during the November migration. Nets, apparently a kind of large trammel, were set in the path of the seals, but the catch depended on the seals staying very close inshore, which often they did not. Seals are still caught from the shore in November in some years, but not many. In the eighteenth century Notre Dame Bay became settled by people who wintered in Newfoundland, and they soon began to exploit the breeding seals in March, first in open boats on occasions when the seals were in sight of land, but after 1794 in decked schooners and brigantines which could go out to the ice and stay there. This developed into the immense sailing fleet of the mid-nineteenth century; in 1857 400 sail took 13,000 men to the ice, and brought back over half a million seals worth more than a million dollars. The effort was spread over a large part of the Newfoundland coastline; St John's and the ports in Conception Bay, notably Harbour Grace and Brigus, were by then the chief sealing ports, though in the earlier days the leaders in the schooner fishery had been Twillingate, Fogo and Greenspond farther north.

The schooners seriously reduced the number of seals, and profits became less. The sealing fleet was halved during the 'sixties, but the fishery itself received a new lease of life with the introduction in 1863 of wooden steamers, which could penetrate the ice in a way impossible for sailing vessels, and so come at the now scarcer seals. The schooner fishery was virtually extinct by the 'eighties, but the steam fleet grew to about 20 wooden ships (of from 300 to 500 tons), based first on Harbour Grace and St John's, and later on St John's alone. This St John's monopoly had the effect of cutting off Bonavista Bay and Notre Dame Bay from the fishery; crews could tramp in from the villages in Conception and Trinity Bays, but there was no way by which men from the more distant outports could reach St John's in mid-winter.

The steamers were on the whole successful. Their crews numbered from 3000 to 5000, and they slaughtered annually about 300,000 seals (more than half the schooner catch with about one-third as many men), but they did not have it all their own way. Stout as they were, no fewer than 39 were lost on the ice between 1871 and 1917, and their sealing careers averaged about 20 seasons. Their last days were prolonged by the introduction, in the early years of this century, of larger steel ships with ice-breaker bows; these were able to relieve the wooden ships of much

of the violent ice-ramming that had formerly been necessary. In the years just before the 1914 war there were nine steel ships and about a dozen of the old wooden fleet pursuing the fishery.

(From now on, see Table 1 and Figs. 2–7.)

By 1919 the fleet was reduced to 10 vessels, and from then until 1931 the number varied between 8 and 12. The depression, which hit Newfoundland as hard as anywhere, reduced the numbers to four in 1932, and brought the number of men below 1000 for the first time (Fig. 2). From this, some recovery was made in the 'thirties, apart from the fact that prices (Fig. 6) remained low after the depression, so that the men received a meagre reward for some not

Table 1. *The Newfoundland Seal Fishery from* 1900 *to* 1948

Year	Vessels	Tonnage	Men	Seals	Seals/man	Value ($)	Price per 1000 skins ($)	Share/man ($)
1900	19	6,053	3760	353,276	94	483,602	1369	43
1901	19	5,898	3836	345,055	90	388,895	1127	34
1902	20	6,468	3978	274,219	69	402,623	1468	34
1903	22	7,199	3378	286,230	85	449,797	1571	44
1904	21	6,655	3328	284,473	86	403,794	1419	40
1905	22	7,165	3532	177,100	50	311,224	1758	29
1906	25	8,634	4061	341,836	84	607,505	1777	50
1907	22	7,968	3685	245,051	67	455,210	1858	41
1908	18	6,814	3141	213,868	68	375,443	1755	40
1909	20	9,464	3580	269,302	75	458,020	1700	43
1910	19	8,994	3364	333,349	99	628,009	1883	62
1911	18	8,727	3973	304,591	77	494,075	1622	41
1912	23	12,670	4179	175,130	42	329,265	1880	26
1913	19	11,472	3609	272,965	76	493,846	1808	46
1914	20	12,067	3959	233,719	59	497,979	2130	42
1915	13	7,878	2932	47,004	16	93,479	1989	11
1916	11	5,916	2028	241,302	119	642,464	2663	106
1917	12	4,390	2131	196,228	92	516,717	2632	81
1918	12	4,250	2056	151,434	74	863,553	5703	140
1919	10	3,599	1719	81,293	47	278,145	3421	54
1920	9	3,354	1583	33,985	21	159,950	4244	34
1921	9	3,440	1264	101,452	80	171,243	1689	45
1922	8	3,150	1196	126,031	105	197,838	1570	55
1923	8	3,150	1224	101,770	83	209,136	2055	57
1924	8	3,150	1227	129,561	106	241,127	1861	66
1925	10	3,899	1505	127,882	85	269,467	2107	60
1926	12	5,033	1648	211,531	128	395,511	1869	80
1927	9	5,125	1634	180,459	110	297,423	1648	61
1928	11	8,637	2190	227,022	104	394,164	1736	60
1929	12	7,152	2154	201,856	94	359,920	1783	56
1930	11	7,047	2129	218,644	103	405,810	1857	64
1931	8	4,863	1268	83,077	66	121,115	1491	32
1932	4	2,651	731	48,613	66	58,367	1200	27
1933	6	4,119	1122	176,046	157	191,912	1089	57
1934	8	4,863	1459	223,700	153	324,792	1452	74
1935	10	6,290	1811	143,031	79	173,754	1214	32
1936	8	4,863	1460	183,689	126	224,495	1222	51
1937	7	4,584	1305	113,340	87	205,022	1809	52
1938	8	5,004	1459	226,747	155	490,664	2164	112
1939	7	4,584	1291	97,345	75	149,399	1535	39
1940	7	4,584	1307	159,687	122	205,030	1283	52
1941	4	1,677	606	42,666	70	67,179	1574	37
1942	2	858	235	4,698	20	11,686	2488	17
1943	0	—	—	—	—	—	—	—
1944	1	458	121	6,697	55	17,683	2639	49
1945	5	480	114	11,543	101	33,621	2913	98
1946	12	1,454	367	34,605	94	121,080	3499	110
1947	17	2,276	628	97,535	155	350,974	3598	186
1948	25	4,261	1035	141,971	137	398,020	2805	128

unsuccessful hunting. Then the second World War, as has been mentioned, reduced the fleet once again and actually stopped sealing in 1943. From the sealers' point of view this was a pity, as the high prices ruling during the war would have brought a good return from a successful season; but the larger ships were wanted elsewhere (and were mostly sunk), and many

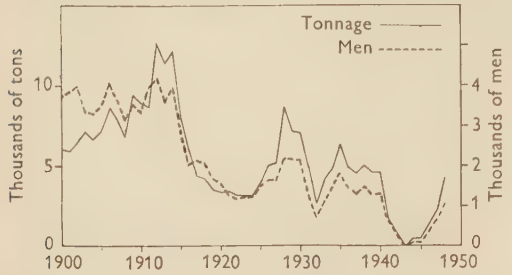


Fig. 2. The size of the sealing fleet, in tonnage and men, from 1900 to 1948.

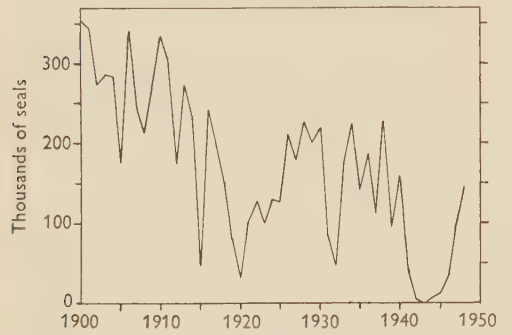


Fig. 3. The number of seals caught from 1900 to 1948.

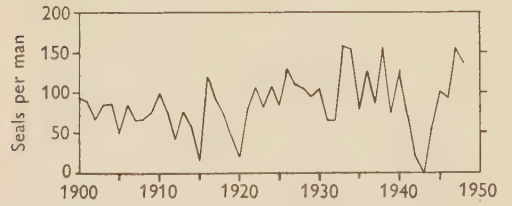


Fig. 4. The number of seals caught per man from 1900 to 1948.

(at the south-western end of the island) (Fig. 1). Except for one vessel they all made good trips, even the tiny *Little Whitecoat* of 9 tons and a crew of eight bringing back over 400 seals. The 91-ton *Mary F. Hyde* from Port aux Basques had the Gulf of St Lawrence to herself, and her crew of 20 brought back 4206 whitecoats weighing 80 tons. This crew killed 211 seals a

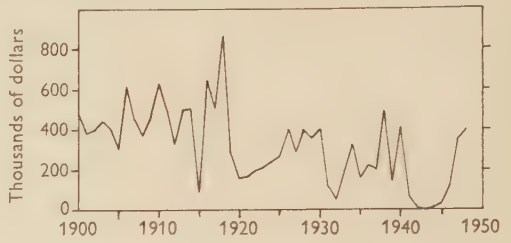


Fig. 5. The total value of the seal fishery, in dollars, from 1900 to 1948.

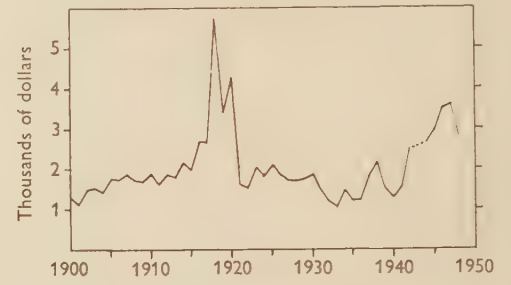


Fig. 6. The price of seal oil, or 'fat', given as the price in dollars per 1000 skins, from 1900 to 1948.

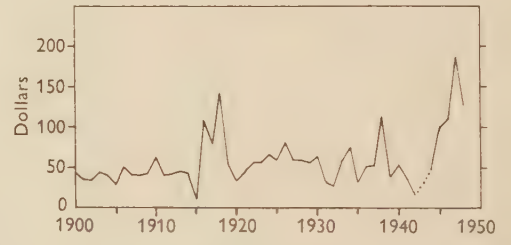


Fig. 7. Share per man, in dollars, from 1900 to 1948. (The men's share is one-third of the value of the catch, divided equally; this is done separately for each vessel.)

of the men were on war service and not available for sealing.

In 1944 the *Eagle* sailed alone from St John's with 121 men and had a moderate trip, catching 6697 seals (Fig. 3) or 55 per man (Fig. 4). Next year no ship sailed from St John's, but five motor-vessels put out from Twillingate (in Notre Dame Bay), Little Bay Islands (near Green Bay, farther west), Port Union (by Catalina on the East Coast) and Port aux Basques

man in 4 weeks at sea, and their share was the high one of $213·55 per man. Three of the other vessels had fair or good trips, and for the fishery as a whole the seals caught per man numbered 101, and the men's share worked out at $98 (Fig. 7).

This was an encouraging start to the new venture, and it is not surprising that in 1946 12 vessels pursued the fishery. The *Eagle* made another appearance, but all the others were motor-vessels, and they had another

successful season, 367 men killing 34,605 seals, or 94 per man. The price of fat (Fig. 5), which had been rising steadily since 1940 when it was $1283 per 1000 skins, had reached $3499, and the men's share was in consequence a high one, $110.

In 1947 the fleet increased again; a second steamer, *Sable Island*, joined the *Eagle*, and there were 15 motor-vessels. Several vessels made two, or even three, trips; the catch on the first trips was mainly whitecoats, the later catches consisting mainly of bedlamers with many adult harps and a few hoods. 628 men brought back 97,535 seals, 155 per man, and since the price of fat had risen once again, to $3598 per 1000 skins, the men's share was the record one of $186. The figure of 155 seals per man has been beaten only once before, by 157 in 1933, and equalled once, in 1938.

The recovery has continued in 1948, with an added feature, namely a fleet of foreign registry nearly as large as that of the Newfoundland ships. This foreign (largely Canadian) fleet sailed from St John's, and most of the crew were Newfoundlanders; occasional vessels of foreign registry have joined in the Newfoundland seal hunt in previous years, but never on such a scale as this. Once again, the largest contingent of Newfoundland ships was sent out by two firms in St John's, but vessels were also equipped by nine concerns in eight outports extending from Port aux Basques to Notre Dame Bay. The tonnage, 4261, and the number of men, 1035, both approached the pre-war figures; the catch of seals, 141,971, was the highest since 1940; the number of seals per man was the good one of 137, and the total value of the catch, $398,020, has been exceeded only once (in 1938) since 1930 (Fig. 5). The price of fat, at $2805 per 1000 skins, had kept up better than in the corresponding period after the first World War, and the men's share averaged out at $128. Two motor-vessels were lost in the ice, and another damaged but towed home with her cargo of seals.

A certain pattern is beginning to emerge from this new phase in the seal fishery. First of all, small vessels are now as successful as the steamers, which was not the case 100 years ago when the schooner fleet had to give way to steam. Secondly, the sealers can catch as many seals per man as ever. Both these facts tend to show that the seals are at least as numerous as they have ever been this century, and the catches of the last few years suggest that the seal herds may have increased during the years of restricted hunting in the second World War. Thirdly, the effort is distributed more widely than before. Until 1942 almost the whole industry was in the hands of two firms, both in St John's. In 1948, nine firms or individuals sent out crews from eight ports scattered from Port aux Basques to Little Bay Islands. St John's remains the most important single port, but the breaking of its monopoly has served to reintroduce the excitements and profits of the seal hunt to the more distant outports; this is likely to be a good thing for Newfoundland both financially and in morale.

The question then arises, can it last? This question originated the previous review of the fishery (Colman, 1937), and the answer then seemed to be that the seals were in no danger of extermination as long as the number of men hunting them remained somewhat below 4000, and even showed signs of increase when the hunters numbered less than 2000. The number of seals is now probably somewhat greater than in 1936, so 4000 can be tentatively given as maximum permissible number of sealers. Now the present motor-vessels average about 100 tons, and their crews number about 25. Some 150 vessels would be needed to take 4000 men to the ice, and such a fleet will not grow overnight; ice-conditions demand specially strengthened hulls, and the existing schooners used in the cod-fishery are not strong enough. Sealers of 100–150 tons, however, should be quite suitable for cod-fishing in summer and autumn, and if this proves to be the case, one of the great handicaps of the steam fleet will have been overcome. The sealing steamers, while too small for general trading, were too large for economical fishing on the banks, and they lay completely idle in St John's harbour for 10 months of the year.

The new sealing fleet has got off to a flying start and is still growing, and there are evidently plenty of seals to support a still larger effort. But there is another factor to be considered, namely the price of fat. After the first World War, the price remained very high until 1920 ($4244 per 1000 skins), but then dropped very suddenly in 1921 to the more normal figure of $1689. In the second World War the price never reached the extraordinary figures of the first World War ($5703 in 1918, $2913 in the corresponding year 1945), but it did increase after the war, reaching $3598 in 1947. In 1948 it fell somewhat but was still, 3 years after hostilities ceased, as high as $2805. It is difficult to foresee what will happen next. Should the price fall to its normal level of about $1500, or sink below it as it did in the depression (it fell to $1089 in 1933), the sealing fleet is not likely to expand very much; but should the price remain high, there is every reason to expect the fleet to increase rapidly. But whatever happens, there is not likely to be any danger to the Newfoundland seal-herds during the next 10 years.

SUMMARY

Newfoundland's fleet of sealing steamers was virtually finished by the second World War, and in 1943, for the first time in 150 years or so, there was no seal hunt. Since then a successful new start has been made with

smaller motor-vessels. In 4 years the fishery has been built up almost to what it was between the wars, and the very high catches per man show that there are plenty of seals. The price of fat, which rose during the war, has kept up for longer than it did after the first World War, and has encouraged the development of the new fleet. By the use of smaller vessels and by the return to the seal hunt of the farther outports, the industry has reverted to some extent to the methods of a century ago, and has broken the monopoly held by St John's; it is to be hoped that this monopoly has been broken for good. The seals do not seem to be in any danger of overfishing, at any rate during the next decade.

REFERENCES

Chafe, L. G. (1923). 'Chafe's Sealing Book: a history of the Newfoundland sealfishery from the earliest available records down to and including the voyage of 1923.' 104 pp. 3rd ed. St John's (Ed. H. M. Mosdell); and annual supplementary sheets up to and including 1948. (From 1940 onwards these sheets have been issued by the Newfoundland Fisheries Board.)

Colman, J. S. (1937). 'The present state of the Newfoundland sealfishery.' J. Anim. Ecol. 6: 145–59.

Nansen, F. (1925). 'Hunting and adventure in the Arctic.' London.

THE FORAGING METHOD OF INDIVIDUAL HONEY-BEES

By C. R. RIBBANDS

Bee Research Department, Rothamsted Experimental Station, Harpenden

(With 9 Figures in the Text)

CONTENTS

	PAGE
1. Introduction	47
2. Technique	47
(*a*) The experimental garden	47
(*b*) Method of marking the bees	47
(*c*) Method of observation and recording	48
3. Results	49
(*a*) Foraging methods of individual honey-bees	49
(*b*) Foraging statistics	59
(*c*) Duration of attachment to chosen crops	60
(*d*) Examples of change of crop	61
(*e*) Effect of weather on time of collection of Shirley poppy pollen	62
4. Conclusions	62
(*a*) The behaviour of the individual honey-bee when foraging	62
(*b*) The basic principle of foraging behaviour	64
(*c*) The circumstances in which bees change from crop to crop.	65
5. Summary	65
References	66

1. INTRODUCTION

The senses used by honey-bees (*Apis mellifera* L.) in the field have been extensively investigated by von Frisch and his school, but the behaviour of the bees under normal foraging conditions has been less adequately investigated, mainly in a quantitative manner. This paper is the result of an attempt to investigate this problem qualitatively by studying the behaviour of a small number of foragers. Most of the conclusions now recorded are derived from studies of pollen-collecting behaviour. The more limited observations of nectar-collecting behaviour have in no instance been found to conflict with the principle derived from the study of pollen collecting, and it is considered unlikely that there is a fundamental distinction between the two types of behaviour patterns.

2. TECHNIQUE

(*a*) *The experimental garden*

The work was carried out on a specially planted plot in the garden attached to the Bee Department at Rothamsted Experimental Station. This plot was sown with Shirley poppies (*Papaver rhoeas*), *Eschscholtzia* 'Orange King', nasturtium 'Tom Thumb' mixed (*Tropaeolum majus*), *Limnanthes douglasii* and *Nemophila insignis*. The Shirley poppies, *Eschscholtzia* and nasturtiums were selected as examples of plants which yield pollen only (the nectar in nasturtiums was not accessible to the honey-bee). *Limnanthes* and *Nemophila* yield both pollen and nectar.

In the centre of the plot there were three large patches, each 20 ft. by 3 ft., and these were planted separately with Shirley poppies, *Eschscholtzia* and *Limnanthes*. These large patches will hereafter be referred to as 'beds'. Along one edge of the plot, and 8 ft. away from the nearest end of these beds, there were three adjoining rows of these same three plants, each row 75 ft. long, and the rows 8 in. apart. These will be called the 'rows'. The nasturtiums and *Nemophila* were planted in sixteen small patches each 2 ft. 6 in. square, planted in the spaces between the main plots. There were also six additional small square patches of Shirley poppies, and three additional ones of *Eschscholtzia*. These small patches will be referred to as the 'squares'. The arrangement of the garden is easily comprehended by reference to the plan in Fig. 1. None of the annuals used for the experiment was being grown elsewhere in the immediate vicinity. The spaces between the flowers were well trampled down by the experimenter, and were occupied by grasses and various hardy weeds not attractive to bees.

(*b*) *Method of marking the bees*

Most workers on bee behaviour have marked bees with paints of various colours, which have been applied to the insect surreptitiously, while it continued with its foraging. This method is convenient for some purposes, but the number of bees which can be marked and recognized as individuals at any one time and place is limited. A more satisfactory method was therefore desirable. A preliminary series of experiments proved that honey-bees lightly anaesthetized with chloroform became rigid and easy to mark, and that they recovered quickly from this anaesthetic with their faculties unimpaired, and exhibited the same

constancy and behaviour towards the flowers of their choice as did a parallel series of marked bees which were not anaesthetized.

The use of this satisfactory anaesthetic enabled bees to be marked with various designs, so that they were easily recognizable as individuals. Several systems were tried, involving markings on both thorax and abdomen, domino patterns on the abdomen, numbers, letters, etc. Thoracic markings were discarded because they ruined the thoracic hairs and might have impaired the pollen-collecting abilities of bees. The tergum of the second visible abdominal segment was finally selected as the most suitable site for the mark, because it was the largest uninterrupted portion of the integument, and paint could be applied there without interference with intersegmental membranes or pollen-collecting hairs. Very small dots were found to be unsuitable because their proportion of edge to surface was too great, and they were frequently rubbed off; domino patterns were discarded for this reason.

Numbers and the alphabet were found rather difficult to apply and the marks used were based mainly upon basic patterns of the alphabet. Their selection was based upon two criteria, that they would be easy to apply and that there would be no possibility of confusion with other marks if they became impaired. The selection of suitable symbols must depend upon the number of bees to be marked—the greater the number the more complicated the design, so that no impaired symbol becomes confused with another complete but simpler one. They were usually applied in either white or yellow cellulose paint, but pale pink and pale blue were also used. Only light colours were readily visible. The paint was a quick-drying model aeroplane dope, and it was thinned to the appropriate consistency with acetone. After the development of this marking system few marked bees were observed in the field with impaired markings. After being marked, the bees were placed in sunshine in a porcelain dish with steep sides, and the very small proportion which did not recover sufficiently to be able to fly away were discarded and destroyed.

(*c*) *Method of observation and recording*

Most of the work was carried out by watching individual honey-bees over long periods, and recording the variety, number and position of the flowers visited, together with the time of arrival and departure of the bee. The rest of the work was done by recording the number and position of marked bees at various times. The beds and the rows of flowers were both staked off and numbered at 1 ft. intervals, and the squares were lettered alphabetically (see Fig. 1).

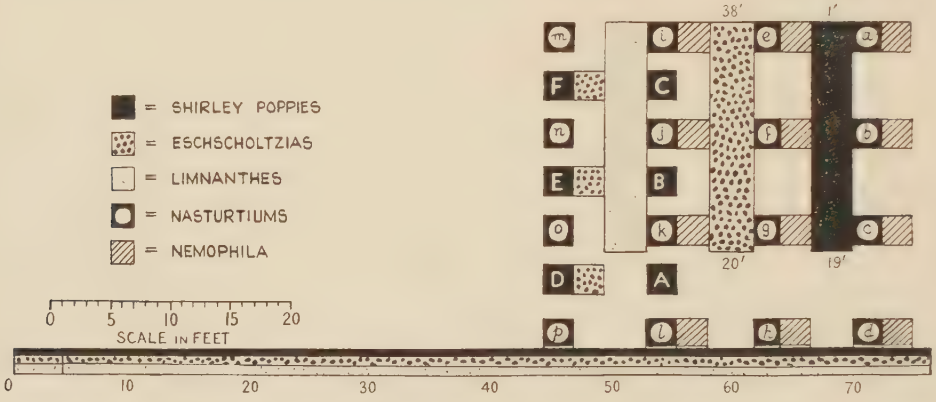


Fig. 1. Plan of experimental garden.

Prolonged observation of individual bees was greatly facilitated by the fact that almost all the observations were made on pollen-collecting bees. Occasionally the arrival of the bee was missed, or she was lost during her trip, and in such cases the size of her pollen load when she was found again provided decisive evidence of her activities when missing.

In order to avoid confusion in these descriptions the term 'trip' is used only to cover the period between arrival on and departure from the foraging area, and 'hive-journey' covers the period between departure from and re-arrival at the foraging area (including all the time spent within the hive). The term 'visit' covers a single visit to an individual blossom, and 'visit sequence' includes all the visits, one or many, made to any area on any one trip.

Time is recorded as Greenwich Mean Time, using

the continental 24 hr. nomenclature. Thus 07.00 hr. was 7 a.m. and 15.30 hr. was 3.30 p.m. G.M.T.

3. RESULTS

(*a*) *Foraging methods of individual honey-bees*

A bee 'A' working on Eschscholtzia

These observations were made on 24 and 25 June, when the *Eschscholtzia* were already blooming well, but there were no flowers on the other plants. On 24 June a single bee was observed working these plants, and this bee was watched for $3\frac{1}{2}$ hr. On 25 June she was watched continuously from 08.00 to 16.00 hr. Although she covered a considerable area observation of her was facilitated by the fact that she was the only bee visiting the experimental plot at this time, and this was the reason why the record of her movements was nearly complete. An abstract from the record is provided in Table 1.

Fig. 3 is a chart showing which portions of her foraging area were visited on each trip. It should be examined in conjunction with Fig. 1, so that the relative positions of the different portions can be visualized. It can then be seen that the central portions of the foraging area (bed 21–32 ft., and row 50–67 ft.) were visited most frequently, and that she visited this region on all but three of the 61 observed trips. The visits to the peripheral portions were the more interesting ones, since they appeared to occur in a non-random manner, e.g. on 25 June six out of seven visit sequences to the lower end of the row (21–49 ft.) were made in the first quarter of the day's foraging. The results of 25 June, as shown in Fig. 3, may be compared with those to be expected if the bee visited each section of the garden with constant frequency throughout the day. The 47 trips were divided into 4 subequal blocks, and a value of χ^2 with four degrees of freedom was calculated for each section. For the four central sections the value of χ^2

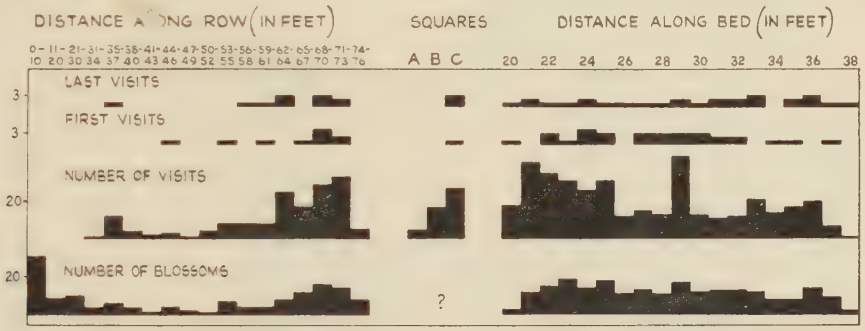

DISTANCE ALONG ROW (IN FEET)
0- 11- 21- 31- 35- 38- 41- 44- 47- 50- 53- 56- 59- 62- 65- 68- 71- 74-
10 20 30 34 37 40 43 46 49 52 55 58 61 64 67 70 73 76
SQUARES
A B C
DISTANCE ALONG BED (IN FEET)
20 22 24 26 28 30 32 34 36 38
LAST VISITS
3
FIRST VISITS
3
NUMBER OF VISITS
20
NUMBER OF BLOSSOMS
20
?

Fig. 2. Analysis of visits of honey-bee *A* to *Eschscholtzia*, 25 June.

The total number of blossoms within her foraging area of 25 June was 321, so on that day she averaged 2·4 visits to each blossom. Although it was not possible to record each visit to each individual blossom, notes were made of occasions when the bee returned to flowers which she had only just left. On eight occasions she flew away, and then returned to the same flower, and on at least 21 occasions she returned to visit a flower which she had visited either two or three flowers back. Five of these 21 visits were to flowers which had received only a brief visit on the first occasion, which indicates that they were accidental. A few blossoms were definitely more attractive than others, and these were usually newly opened ones—one flower was visited four times in six successive visits, and another three times in four successive ones.

This bee did not start or finish her trips at any fixed point, and examination of the histograms in Fig. 2 shows that the flowers to which she made her first and last visits were scattered throughout her foraging area.

ranged from 2·31 to 8·30, whereas the peripheral sections gave values of 9·34, 9·44, 12·74, and 19·13; the 5 and 1% probability levels are 9·49 and 13·28 respectively. These figures indicate that while the bee visited the central area with roughly constant frequency she preferred different peripheral areas at different periods of the day.

A tendency to continue foraging in a definite direction was displayed on most of the foraging trips, so that the bee covered a greater length of her foraging area than she would have done if there had been no continuity of direction. This feature is best illustrated by examples. In the main bed there were on average 13 blooms per foot run, and a total of 224 blooms, of which the bee would visit less than 10% on any one trip. Each blossom visited was recorded by the numbered foot interval, and selected examples of records on 25 June are:

(*a*) 3rd trip: 29, 29, 29, 29, 25, 25, 24, 22, 22, 22, 22, 21, 21, 20, 20, 21, 27, 28, 29, 29, 31.

Table 1. *Foraging statistics, pollen collectors*

Bee	Source	Date	Temp. at 09.00 hr. (° F.)	Foraging times (hr.)	No. of trips	Mean duration (min.)		Mean no. of blossoms visited per trip	Estimated flower visits			
						Trip	Hive-journey		Per hr.		Per day	
									Total	Fruitful	Total	Fruitful
A	*Eschscholtzia*	25. vi.	51·0	08.33–15.41	47	3·8 ± 0·6 Range 3 to 5	5·2 ± 1·6 Range 3 to 11	15·9 ± 4·0 Range 7 to 22	106	72	758	515
F	*Eschscholtzia*	25. vii.	56·0	13.24–13.56	3	(6, 6 and 7)	(7, 6 and 6)	(70 and 82)	450	?	.	.
B	Shirley poppy	14. vii.	70·2	07.00–09.48	19	5·1 ± 1·1 Range 3·5 to 6·5	3·9 ± 1·2 Range 2 to 6·5	6·7 ± 4·4 Range 1 to 16	45		.	.
		16. vii.	71·0	06.36–08.34	14	4·5 ± 1·0 Range 3 to 6·5	4·3 ± 2·0 Range 3 to 11	14·3 ± 5·4* Range 6 to 22	100		.	.
D	Shirley poppy	15. vii.	70·1	06.34–09.00	10	8·3 ± 1·0 Range 6·5 to 10	8·2 ± 1·6 Range 5 to 11	19·3 ± 5·0 Range 14 to 27	77		.	.
C	Nasturtium	8. viii.	40·0	07.28–15.11	21	12·7 ± 2·6 Range 8 to 18	9·2 ± 2·0 Range 7 to 13·5	119·1 ± 28·3 Range 66 to 178	323	175	2457	1130

* Not including trips to the uncapped blossom.

(*b*) 21st trip: 35, 35, 33, 32, 31, 29, 28, 25, 25, 23, 23, 21, 21.

In the first instance the bee went to the end of the bed, and then returned back along it, in the second she taken was the same as, or opposite to, the previous direction. Analysis of all the foraging on this bed shows that of 203 occasions when the bee moved from one foot width of patch to another there were 16

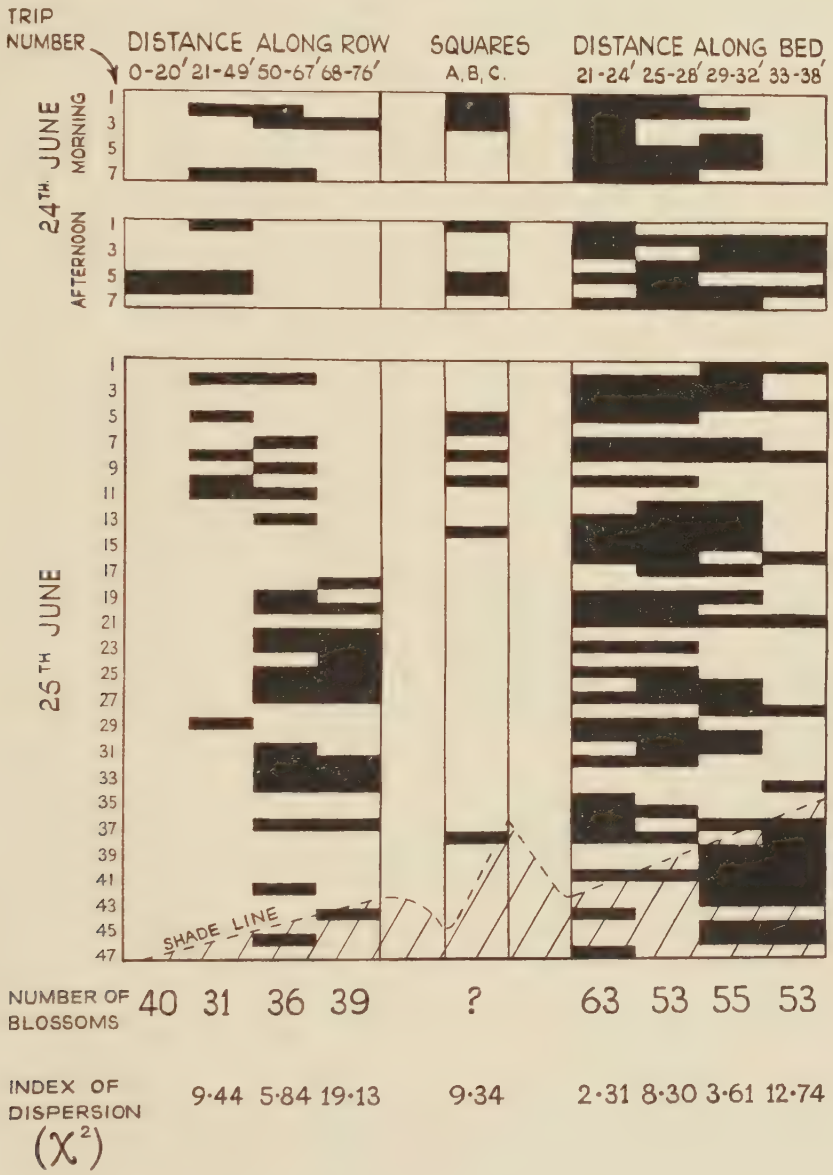


Fig. 3. Visits of honey-bee *A* to *Eschscholtzia*. Portions visited on each trip.

went almost from end to end. Non-directional visiting would have caused an equal tendency for each visit to have been either higher up or lower down the bed than the previous one, and an approximately equal number of occasions on which the direction occasions when she had to reverse her direction, having arrived at the end of the bed; of the remaining 187 occasions, she continued in her previous direction of travel on 155, and changed her direction on only 32.

From 13.40 hr. onwards the main bed gradually became shaded, but the shading of portions of the patch had no direct effect on the foraging. She continued to visit the shaded and unshaded portions of the bed indiscriminately, and there was no tendency to prefer the sunny portion to the shaded one. Fig. 3, which shows the portions shaded and the visits made, illustrates this.

also closing. The gradual closing of the blossoms made the bee much more restless and erratic, so that instead of going contentedly from flower to flower, visiting flowers quite close to each other, she had a marked tendency to jump long distances from one portion of her foraging area to another. This made it much more difficult to follow her activities. I think that this response to unfavourable conditions by increased

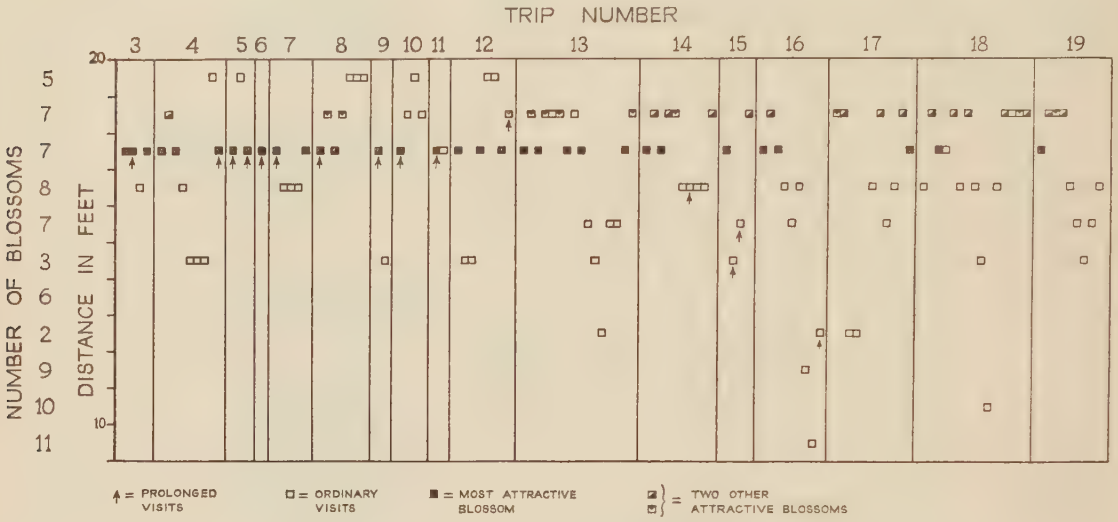


Fig. 4. Visits of honey-bee *B* to Shirley poppies, 14 July.

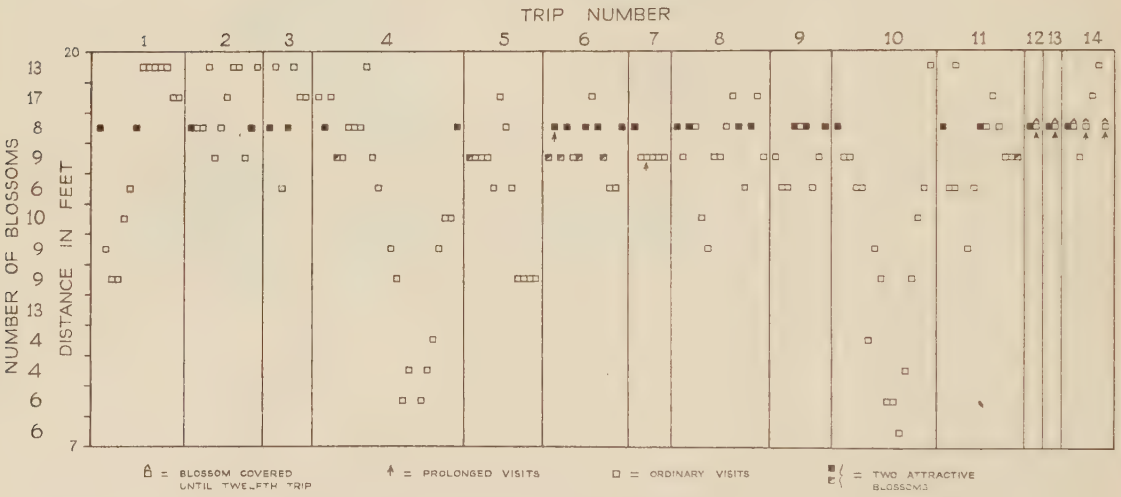


Fig. 5. Visits of honey-bee *B* to Shirley poppies, 16 July.

Shade, either directly or through its effect on temperature, accelerated the closing of the blossoms (the youngest and most attractive ones closing first), but it was not the only factor active in this respect because by 15.30 hr. the blossoms in sunlight were

activity is a normal feature of bee behaviour, and is the mechanism through which they come to concentrate on the more attractive portions of their foraging area, and to change their foraging area when necessary.

I also noticed that (except at the end of the day) the bee usually left the one patch for another after visiting a flower on the edge of a patch. She then took off and flew in a curving path until she found other flowers to visit.

A bee 'B' working upon Shirley poppies

B was watched while working Shirley poppies on the mornings of 14 and 16 July. The results are presented in Table 1, and Figs. 4–6. These observations must be considered in relation to the fact that there were more than 100 newly opened blooms on the bed of poppies on which this bee was foraging, and they were probably being worked by more than 50 bees. The distribution of the available blossoms varied on the 2 days (Figs. 4, 5).

Observations on 14 July showed that *B* was extremely constant to one particular flower, which she visited on every one of her 19 observed trips and 31 times in all. Only two of these trips (at the end of the morning) were begun on another flower. During her earlier visits this flower was also being visited by other bees, but by alighting upon them she attempted, sometimes successfully, to drive them off; at one time there were four bees upon this one flower. During her later visits there were few other visitors, which quickly left. For 11 successive trips she spent nearly all her time upon this one blossom, and one trip was entirely spent upon it (Fig. 4). When this flower had ceased to satisfy she at first returned to it at every second or third flower visit, but she soon came to prefer other flowers and on her last three trips she returned only once per trip. With the failure of the original source the number of visits per trip and the area covered per trip both increased, but much of her attention was concentrated upon two attractive flowers in the adjoining foot width (Fig. 4). Fifty-eight of her 117 flower visits of this morning (and a much higher proportion of her time) were concentrated upon three preferred blossoms (Fig. 6).

B was watched again on 16 July. At 06.35 hr. she alighted on a flower on the plant which had produced her previous favourite. She continued to pay marked attention to this one flower, and commenced 10 of her 14 trips upon it and the others within 1 ft. of it (Fig. 6), but she covered a wider area and visited many other flowers in order to obtain her pollen loads, and made only one very prolonged visit to her new favourite (Fig. 5). At the beginning of this day's observations an attractive flower in the vicinity of her 'landmark' had been covered with a paper bag, so that it could not be visited, and this bag was removed at 08.15 hr., when the pollen supply was diminishing. *B* returned to her 'landmark', then went straight to this newly uncovered blossom, and stayed upon it for the rest of her trip. Her next trip was similar. The following trip was her last one. She went first to the 'landmark', then to the uncovered flower. The latter was now not so attractive, and she went off to visit other flowers, but found them even less suitable and returned twice to the uncovered flower, from which she obtained most of her load. During this last trip she made long prospecting flights over the bed while pollen packing, but usually returned without landing on any other flower.

No further detailed observations of this bee were made, but in the course of other experiments she was recorded as follows:

17 July On bed (twice) and upper row (once)
18 July On upper row (twice) and square A (once)
23 July On square B (four times)
24 July On bed (once), upper row (once), square B (once) square C (once).

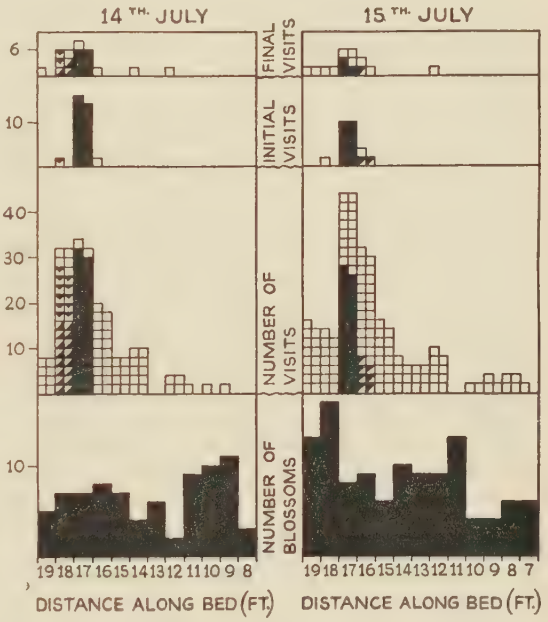


Fig. 6. Analysis of visits of honey-bee *B* to Shirley poppies. Individual blossoms marked as in Figs. 4 and 5.

She provided the longest record of attachment to Shirley poppies (11 days), and it is therefore probable that the first recorded day was also the first day of her visiting. This particular bee changed and apparently extended her foraging area during the course of her visiting. This was not associated with any decline in the quantity of blossom in her original foraging area, which actually increased during this period.

A bee 'C' working upon nasturtiums

This bee was watched during five trips on 7 August, and throughout the day on 8 August, and an abstract

of the results is provided in Table 1. On 19 of her 26 observed trips her first visit was to square L, and of the remaining seven trips the first visit was observed four times, always on the adjoining squares P and H. Although so many of the trips commenced on square L, and the bee usually returned to one particular quarter of that square, she did not alight on any particular flower and occasionally alighted first on a leaf.

Of her observed visits 41 % were to square L, and 34 % to square P: 75 % of her visits were to either squares L or P, and 95 % were confined to the four squares K, L, O, and P. Fig. 7 shows the number of times she went to each square at each trip. It will be seen that both squares L and P were visited on almost every trip. The squares were approximately equal in total blossom (each with 16 nasturtium plants and approximately 250 flowers), and equidistant, but it was clear that the bee was not foraging in a random manner from her starting-point at square L. She went very frequently to square P, much less frequently to squares K and O, and only very occasionally to either squares G or H, which were just as close to her usual starting-point at square L. When on another square she had a marked tendency to return to square L instead of going farther afield. Several other marked bees foraging on nasturtiums at the same time showed marked preferences for other squares, including K and G, and so I do not think that in this instance the recorded preference was associated with any special superiority of square L. In the afternoon of 8 August her foraging area was more limited than in the morning, and squares other than P and L were visited much less frequently. This was despite the fact that in the afternoon she was one of only two bees working on the nasturtiums, while in the morning 13 bees were working these squares. In all her 26 recorded trips square N was visited only three times, and square J only twice, yet four of these five visitings occurred on two consecutive trips (cf. with behaviour of bee on *Eschscholtzia*).

A bee 'D' working on Shirley poppies and Limnanthes

This bee was marked on 12 July, and observed on 14 July to be working on Shirley poppies at square A in the morning and on *Limnanthes* in the late afternoon. Unlike most of the bees working *Limnanthes*, and the rest of the several observed on both *Limnanthes* and pollen plants, she was gathering nectar only from *Limnanthes*. She was never seen to gather pollen from this plant.

On 15 July she was observed from 06.30 hr. onwards. Her first observed trip (of which the results are incomplete) included visits to square A, the centre of her foraging area on the previous day, but this square was not visited on subsequent trips. On her second trip she went to the blossoms near to or on which she remained for the rest of the morning. As she was foraging upon the row of Shirley poppies it was possible to record each visit to each individual flower. A record of these visits is presented in Fig. 8. This shows how on her first and second trips she sampled different portions of the crop, how she 'attached' herself to a suitable portion, and paid most of her attention to two adjacent flowers for the next three trips, and how she then became erratic and covered a wider area, visiting her erstwhile favourite blossoms at intervals, until the *Limnanthes* began to yield. Discrimination by the bee is demonstrated by the very great differences in the numbers of visits to neighbouring flowers, five adjoining blossoms having received 19, 0, 8, 27 and 28 visits per flower. The first and last visits of each trip of this bee were not concentrated upon any one flower, but were scattered throughout her foraging area.

Although seen on *Limnanthes* on the previous evening this bee did not alight on these plants during her first seven observed trips, and it was not until 08.20 hr. that she visited one blossom. This was apparently unsatisfactory, and she returned to Shirley poppies. Two trips later she interspersed her visits to the poppies with a visit to a *Limnanthes* flower and four visits to *Eschscholtzia*, and, later, one more visit to an *Eschscholtzia*. Then on her next or eleventh trip she visited Shirley poppies, then six *Limnanthes*, then returned to Shirley poppies, then to seven *Eschscholtzia*, and then to *Limnanthes*, which she at last preferred and to which she made 210 visits before finishing her trip. She finished this trip at 09.42 hr., and had not returned by 10.50 hr., when observations ceased. At 15.45 hr., when I was revisiting the garden to pick off dead blossoms, I saw this bee return to *Limnanthes*, and watched her until 18.15 hr., when she was the last bee to leave the garden. Next day she was seen on Shirley poppies in the morning, but not watched. In the afternoon she was seen gathering nectar from *Limnanthes* at 12.50 hr., and watched until 15.15 hr. She did not attempt to visit any Shirley poppy flower on these afternoon trips.

A bee 'E' which worked on Limnanthes *and* Eschscholtzia, *Shirley poppies and* Nemophila

(1) Collecting from *Limnanthes* and *Eschscholtzia*. This bee was caught on nasturtiums, and marked in the late afternoon of 24 July. On the following morning it was seen on *Eschscholtzia* at 07.52 hr., and then on the row of *Limnanthes* at 08.00 hr., carrying a load of *Eschscholtzia* pollen. It returned empty to the *Limnanthes* at 08.24 hr., and continuous observations were made on its foraging area until 16.50 hr. The bee was last seen at 15.09 hr. During this day this bee made 14 trips, and collected pollen from *Eschscholtzia* and both pollen and nectar from *Limnanthes*. The bee was observed behaving similarly

on the next day, 26 July, and continuous observations were made between 07.50 and 09.16 hr., during which time five trips were completed.

The main foraging area of this bee covered a length of 40 ft. along the row where blossoms of both *Limnanthes* and *Eschscholtzia*, growing in adjoining rows, were intermingling. This area contained about 2000 *Limnanthes* flowers and 500 *Eschscholtzia* flowers. In addition she visited the bed of *Limnanthes* four times, the bed of *Eschscholtzia* once, and the nearest square of *Eschscholtzia* twice.

noon the proportion of *Eschscholtzia* decreased, at first gradually and then very rapidly, until on the last visit it had dropped to only 0·2 %. Next morning the proportion of *Eschscholtzia* steadily increased from 17 % on the first visit to 73 % on the fourth visit and then started to decline again, and was only 44 % on the fifth visit. I think that the much quicker increase of the *Eschscholtzia* proportion on 26 July, and its subsequently quicker decline, was associated with a difference in the weather of the 2 days. On 25 July there was a drizzle until 07.00 hr., and the sun did not

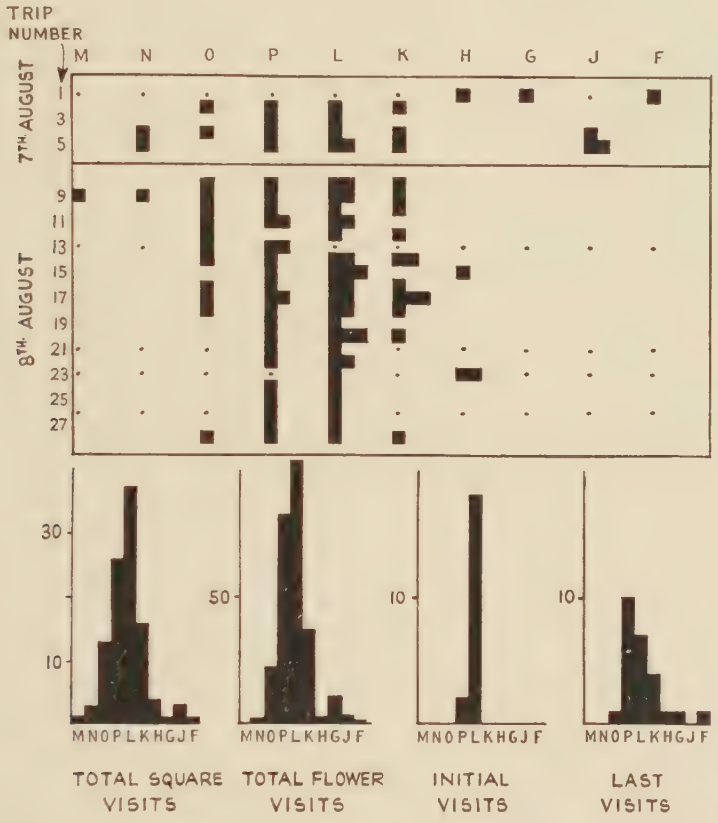


Fig. 7. Visits of honey-bee *C* to nasturtiums. Dots represent trips incompletely observed. In the upper diagram each square represents a single visit-sequence, each rectangle represents two or more.

The chief interest of this series of observations lies in the varying proportions of the blossoms of the two plants which were visited by this bee at different times of the day, and in Table 2, which contains a précis of the observations, the frequency with which she changed from one type of flower to the other is recorded.

The record of 25 July shows that during the morning the proportion of *Eschscholtzia* flowers visited increased from less than 40 % in the early visits to a maximum of 61 % in the sixth trip. During the afternoon until 07.25 hr., but the morning of 26 July was fine and sunny throughout. I ascribe these wide and consistent variations in the proportions of the flowers visited to choice by the bee, following changes in the relative attractiveness of the blossoms. Evidence that there were marked diurnal changes in the yield from both species of flowers is provided by reference to the details of the individual trips. The morning shortening of the visiting period from about 20 min. to 7–8 min., coupled with a reduction in the number of flower visits required to obtain a load and an increase

Table 2. *Foraging of the bee 'E' upon* Limnanthes *and* Eschscholtzia

	Trip no.	Trip starting time	Duration (min.) Trip	Duration (min.) Subsequent hive-journey	No. of flowers visited L	No. of flowers visited E	Percentage E	Foraging sequence
25 July	1	07.52	?	?	?	?		Seen on E and then on L
	2	08.24	19	10		44	37	*r*E 26 3 9 3 1 2
					43			*r*L 6 11 4 12 6 4
					33			*b*L 33
	3	08.53	23	9		21	14	*r*E 1 1 1 1 1 4 3 15 1 3
					68			*r*L 10 9 7 5 6 4 6 7 12 2
					66			*b*L 66
	4	09.25	20	10		26+	41	*r*E 1 1 1 1 1 3 3 1 1 [Lost for 7 min.] 3 7 3
					37+			*r*L 10 2 2 3 5 1 7 1 2 [Lost for 7 min.] 1 2 1
	5	09.55	7	8		26	49	*r*E 3 4 2 1 2 1 4 3 2 1 1 1 1
					27			*r*L 4 2 2 1 2 3 1 1 6 1 1 2 1
	6	10.10	8	7		30	61	*r*E 1 1 7 4 7 4 1 2 3
					19			*r*L 4 2 1 4 3 1 1 2 1 1
	7	10.25	10	15		27	51	*r*E 1 1 1 1 1 1 2 2 2 2 1 2 5 2 3
					47			*r*L 2 11 3 5 1 1 3 2 7 1 1 4 1 1 4
						2		*a*E 2
					20			*b*E 20
	8	10.50	7	7		26	55	*r*E 4 6 1 5 1 3 2 1 2 1
					21			*r*L 3 1 2 3 1 4 1 4 2
	9	11.04	8	8		16	24	*r*E 2 1 1 1 1 1 1 1 1 2 1 1 1 1
					52			*r*L 1 4 1 1 6 2 2 12 1 1 4 12 1 4
	10	11.20	12	8		11		*r*E 4 4 1 1 1
					64		13	*r*L 4 5 1 50 3 1
						8		*b*E 8
	11	11.40	27	16		30+	12	*r*E 1 1 1 1 1 1 1 1 1 1 1 1 9 1 1 [Lost for 4 min.] 2 1 1 1 1 1
					220+			*r*L 3 56 6 8 11 1 9 24 3 3 3 4 1 14 1 11 [Lost for 4 min.] 13 9 7 19 1 13
	12	12.23	66	8		17	2	*r*E 6 1 1 1 1 1 1 2 1 1 1 1
					713			*r*L 85 52 4 23 1 3 22 278 41 87 32 85
	13	13.37	86	15		5	0·5	*r*E 9 1 1 1 1 1
					936			*r*L 5 3 93 370 243 113 100
					58			*b*L 56 2
	14	15.18	51			1	0·2	*r*E 1
					533			*r*L 3 530
26 July	1	07.50	18	6		16+	17	*r*E 1 [Lost for 4 min.] 2 2 1 10
					81+			*r*L 62 8 [Lost for 4 min.] 6 4 1
	2	08.14	8	10		20	33	*r*E 2 2 1 1 6 3 1 2 1 1
					40			*r*L 3 1 17 2 6 1 1 1 1 7
	3	08.32	8	7		24	48	*r*E 4 12 1 3 2 1 1
					25			*r*L 2 1 5 13 3 1 1
	4	08.47	7	8		33	73	*r*E 7 1 1 5 12 3 4
					12			*r*L 1 1 1 2 2 4 1
	5	09.02	14			42	44	*r*E 2 1 1 1 1 1 1 1 1 1 5 3 1 1 1 5 1 1 2 4 3 1 3
					54			*r*L 11 2 1 2 1 1 1 1 2 1 13 3 2 1 1 1 2 1 3 1 1

Abbreviations: L = *Limnanthes*, E = *Eschscholtzia*, *r* = row, *b* = bed, *a* = square A.

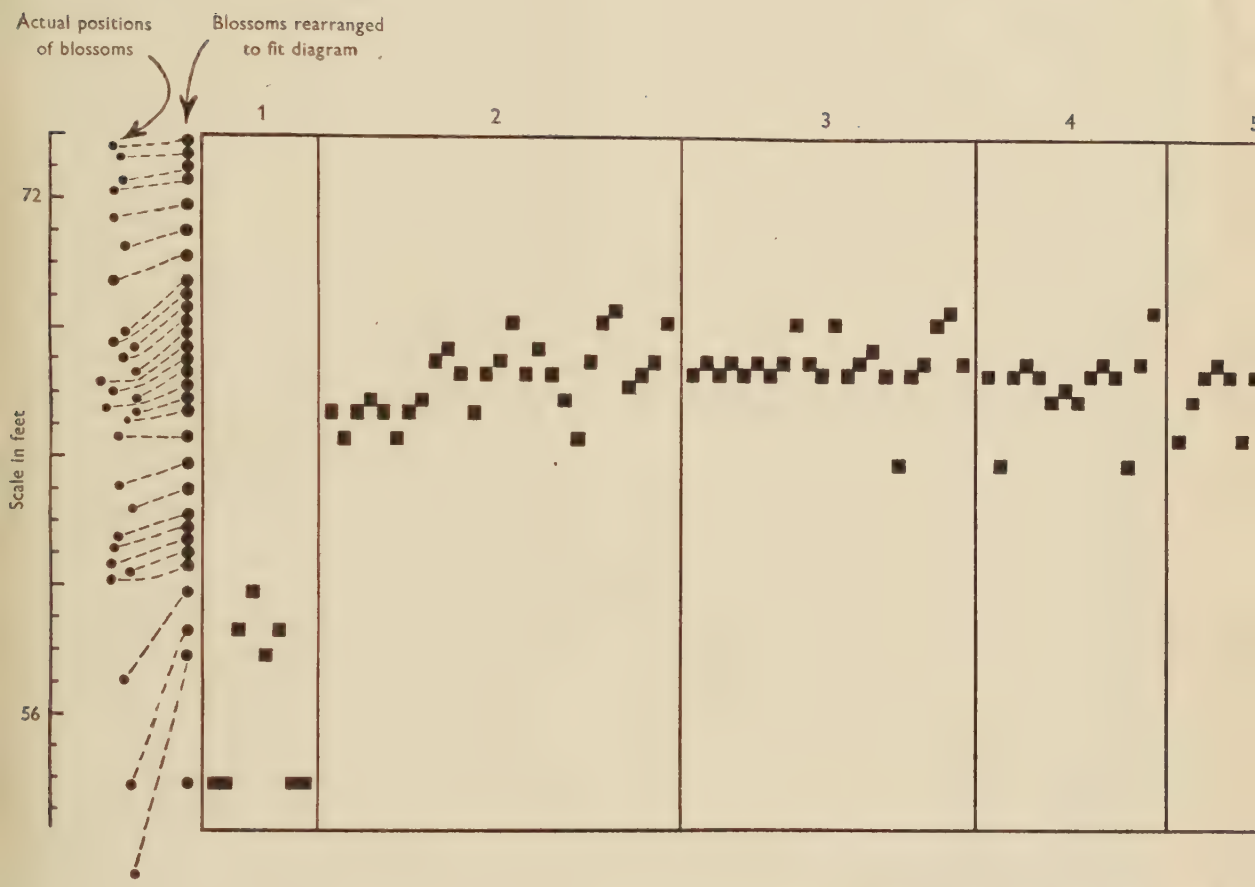


Fig. 8. Visits of honey-bee *D* to Shirley poppies,

(This diagram may be m

Table 2. *Foraging of the bee 'E' upon* Limnanthes *and* Eschscholtzia

in the proportion of visits to the pollen bearing *Eschscholtzia*, can be ascribed to an increased availability of pollen from the *Eschscholtzia*, and possibly from the *Limnanthes* also. The quickness of the change in the journey time indicates the probability that this pollen suddenly became more freely available (no study of another dehiscence was made). In the late morning of 25 July a falling off in the quantity of *Eschscholtzia* pollen available (the competition for this pollen was much greater than during the experiments made in June) was at first compensated for by an increase in the quantity of nectar and/or pollen available from *Limnanthes*, and the bee managed to secure two loads in a short time mainly from the latter plant. Then from 11.30 hr. onwards the yield from *Limnanthes* apparently fell off rapidly, and at each journey the number of flowers visited and the time taken increased considerably. The last complete load required 994 visits to *Limnanthes* and five visits to *Eschscholtzia*, and took 86 min. to collect.

The data indicate that while there were periods when the bee seemed to visit both kinds of flowers indiscriminately, she usually showed a preference for either one species or the other.

Examination of the data concerning the frequency with which she changed her choice of flowers (Table 2) provides evidence concerning the means by which this choice was exercised.

On 25 July at the beginning of her third trip she turned to *Eschscholtzia* on five successive occasions, visiting one flower only and then returning to several *Limnanthes*. At her sixth attempt she apparently alighted on a more satisfactory *Eschscholtzia* blossom, and from then onwards during her next four trips visited the blossoms of both species in fairly equal numbers. However, she paid 15 successive visits to *Eschscholtzia*, followed by 12 successive visits to *Limnanthes*, and there were three spells during which she paid a long succession of only single visits to the *Eschscholtzia*. This is not in accordance with the expectation of a random distribution. The most informative results were obtained during her afternoon trips. On her ninth trip she showed a definite preference for *Limnanthes*, and all her visits to *Eschscholtzia* were to single flowers only. On the tenth trip she made 50 successive visits to *Limnanthes* on one occasion, and she certainly obtained most of her supplies from this species. The eleventh trip is the most interesting one. After 56 successive visits to *Limnanthes* there was a period when she alternated between visiting small numbers of *Limnanthes* and single blossoms of *Eschscholtzia*. She then apparently found more suitable *Eschscholtzia*, and visited nine in succession before going back to her previous routine. On her twelfth trip she paid six successive visits to *Eschscholtzia*, after a run of 85 successive visits to *Limnanthes* and before a run of 52. For the rest of the day her trips comprised visits to *Limnanthes*, interspersed with single visits to *Eschscholtzia* at less and less frequent intervals. The increasing number of flower visits and length of each trip provide evidence that the *Limnanthes* were becoming less productive, but the single visits to the *Eschscholtzia* indicate that at each time of sampling the bee found them wanting. When the bee arrived next morning she at first continued with her methods of the previous afternoon, and paid 62 successive visits to *Limnanthes*, but on visiting the *Eschscholtzia* she evidently found them more satisfactory, and subsequent visits became more and more frequent.

I conclude that having visited a satisfactory source of supply the bee tended to remain upon flowers of that species; after an unsatisfactory visit she tended to turn to the other species. The extent of this tendency to change was determined by her memory of the relative yields from both species in the immediate past.

(2) *Collecting from Shirley poppies and* Nemophila. There were no observations on Sunday 27 July, but on 28 July the same bee was seen at 07.07 hr. to make unfruitful visits to three squares of *Nemophila*, and then to collect pollen from Shirley poppies. The bee was watched until 12.57 hr., when she was driven away by continuous rain, and a record of her movements is presented in Table 3. It will be seen that she was observed to collect at least four complete pollen loads from Shirley poppy, and that she interrupted both the first and the third of these trips in order to inspect the *Nemophila*, with negative results. She was then lost for a short period, and found again at 08.15 hr., working on *Nemophila* but carrying a large load of (?) Shirley poppy pollen. She paid no further attention to Shirley poppies that morning, although counts showed that other bees were still working this crop (there were 39 on it at 07.30 hr., 79 at 08.00 hr., 44 at 08.30 hr., and 15 at 09.00 hr.). She did not, however, pay exclusive attention to *Nemophila*; on her 08.15–08.42 hr. trip she visited the main bed and the row of *Limnanthes* (her foraging area 2 days previously) and was seen to visit 59 flowers of *Limnanthes* and 61 of *Nemophila*. On each of her three subsequent trips she visited some *Limnanthes* flowers, but the proportion decreased rapidly and on her last two trips she visited only 12 flowers of *Limnanthes* to 507 of *Nemophila*. On her last visit she also alighted on and inspected one flower of wild marguerite which was growing near her route, but she did not gather anything from this.

This bee was not seen on 29 or 30 July (both dull days) but she was seen (for the last time) three times on 31 July, visiting Shirley poppies. Presumably she had by this time transferred her main attention to a more satisfactory crop growing elsewhere.

It was interesting to note that the bee's first visits on

Table 3. *Foraging of the bee 'E' upon Shirley poppies*, Limnanthes *and* Nemophila, 28 *July*, 07.07–12.30 hr.

Trip	Duration (min.) Trip	Duration (min.) Subsequent hive-journey	No. of flowers visited P	No. of flowers visited L	No. of flowers visited N		Foraging sequence
1	5	11	11			P	11*b*
					4+	N	1*g* 1*f* 1*e* 1*g*
2	5	9	5+			P	2*r*...3*b*
3	4	7	11			P	7*b* 2*b* 2*r*
					1	N	1*g*
4	?	?	3+			P	2*r* 1*b* ...
5	27+	15	?		61+	N	[First seen with large load] 23*g* 7*f* 17*c* [Lost for 3 min.] 2*g* 12*c*
				59		L	56*b* 3*r*
6	88	20			394	N	23*g* 19*f* 4*g* 18*g* 32*g* ... 32*g* 1*k* 143*g* 111*f*
				66		L	45*b* 7*b* 9*b* ... 14*b*
7	73	11			396	N	239*b* 2*g* 4*k* 10*g* 36*f* 7*e* 26*g* 12*g* [Lost for 14 min.] 22*g* 32*f* 1*e*
				4		L	2*b* 2*b*
8	21+				111	N	28*g* [Lost for 1 min.] 14*d* 5*g* 20*g* 32*d* 2*g* 4*f* 6*b* away in rain
				8		L	2*b* 1 marguerite

Abbreviations: P = Shirley poppies, L = *Limnanthes*, N = *Nemophila*, *r* = row, *b* = bed, *c*, *d*, *e*, *f*, *g*, etc. = squares.

28 July were to the *Nemophila* patches which she had presumably worked on the previous day, and that she transferred her attentions temporarily to the poppies when she found that *Nemophila* was not yet yielding. This accords with her behaviour on 26 July, which commenced with a long succession of visits to *Limnanthes*, which had been most satisfactory on the previous afternoon.

Inspection visits to previous crops were an important feature of her behaviour. For instance, she inspected *Eschscholtzia* when she was working *Limnanthes* on the afternoon of 25 July, and on 28 July she first inspected *Nemophila* when she was working Shirley poppies, and then inspected *Limnanthes* while she was gathering from *Nemophila*.

(*b*) *Foraging statistics*

(1) *On pollen-yielding crops*

A summary of the pollen-collecting statistics is presented in Table 1. Bees working Shirley poppies collected pollen from every flower visited (occasional flowers were inspected without alighting) but 32 % of the visits to *Eschscholtzia* on 25 June and 54 % of the visits to nasturtiums were unfruitful. There was great variation in the time spent on individual fruitful blossoms.

The record from *Eschscholtzia* on 25 June was obtained under optimum conditions, when the new crop had not been found by other foragers—a month later competition was intense and this would explain the greater number of blossoms visited and the longer foraging times of *F*.

Under the optimum conditions the trip times of *A* showed little variation through the day, but the hive-journey was somewhat less constant. During Shirley poppy recordings competition was very keen, and these trips were definitely quicker towards the middle of the foraging time, and took up to 50 % longer near the beginning and end. The lengthening at the end was the consequence of pollen shortage, as it was eliminated on 16 June when *B* worked a previously capped blossom. Differences between the times of consecutive trips were small, but there was a marked difference between the average times of two different bees, *B* and *D*, when working in similar conditions.

The foraging times accord quite well with those of Park (1928), who observed individually-marked bees as they returned to their hives after collecting maize pollen. He obtained records of an average of six to eight and a maximum of 20 trips in a morning. Under optimum conditions Shirley poppy and *Eschscholtzia* foragers could exceed this maximum; the 47 trips now recorded in one day from the latter plant are twice the maximum number hitherto recorded for any bee foraging on plants.

I am not aware of any comparable published data concerning the number of blossoms visited by pollen gatherers. Vansell (1942) stated that 84 visits were required to gather a pollen load from pear, and more than 100 visits for a pollen load from dandelion; this latter figure may not be typical because on 3 May 1947 I watched a marked bee while she gathered six consecutive loads of pollen from dandelion, and the number of blossoms she visited per trip varied between 8 and 32, average 18·3. The records in Table 1 show that when pollen is abundant loads are obtained very quickly; it must be remembered that the number of flower visits per hour or per day is not an index of the pollinating capacity of the bee, whose foraging frequently consists mainly of oft-repeated visits to favourite flowers. This factor is even more forcibly applicable to nectar collectors; in both instances the number of blossoms in the foraging area is a more correct index of pollinating capacity than the number of flower visits.

(2) *On nectar-yielding crops*

Although the main purpose of these experiments was to study the pollen-collecting behaviour of the honey-bee some information was gathered about its behaviour when gathering nectar only, or nectar and pollen, from *Limnanthes* and *Nemophila*.

There are five nectaries to each *Limnanthes* blossom, all of which were usually visited. There were two records of the time taken by *D* to collect a load of nectar only from *Limnanthes*. One load took 106 min. to collect (from 13.29 to 15.15 hr.) and involved 1446 visits to *Limnanthes* blossoms. Another load, possibly incomplete, took 150 min. to collect (from 15.45 to 18.15 hr.) and involved 1110 visits. The afternoon load took less time to collect although it involved more visits. During the collection of the afternoon load the times taken to visit successive batches of 200 blossoms were recorded. These times were at the rate of $5\frac{1}{2}$, $6\frac{1}{2}$, 7, 6, 8, 8, and $9\frac{1}{2}$ min. per 100 flowers, and the last 100 were collected in 11 min. The evening load was collected at the rate of $13\frac{1}{2}$ min. per 100 flowers. These times show a progressive increase. The decrease in rate was definitely not associated with increasing yield, and I think that it was related to decreasing temperature.

The few records of pollen and nectar collection from *Limnanthes*, by *E* (Table 2), are reduced in value by the fact that this bee spent a proportion of her time gathering from *Eschscholtzia*. However, the data indicate that the latter plants were not a useful source of supply from 11.40 hr. onwards. The three full loads collected after this time occupied 27, 66 and 86 min. per trip, and involved visits to 250, 730 and 999 blossoms. These marked increases in both number of flowers visited and the duration of each trip indicate a progressive decrease in yield per flower.

E was again observed 2 days later while gathering pollen and nectar mainly from *Nemophila*. One load, almost entirely from *Nemophila*, took 73 min. to collect and involved 400 flower visits. Another bee was watched for one trip on 16 July, when working *Nemophila* only for both nectar and pollen. This trip commenced at 13.38 hr., occupied 51 min. and involved 348 flower visits.

These figures indicate that these nectar gatherers were making from about 300 to 1000 flower visits per foraging hour, and compare with the observed rates of from about 50 to 175 fruitful flower visits per hour of the pollen gatherers.

(*c*) *Duration of attachment to chosen crops*

Although the Shirley poppies always attracted large numbers of bees it was soon found that the composition of this bee population was changing very frequently. Of 10 bees marked on this crop on 7 July, five were present on 10 July, and none on 16 July. Daily observations were not made during this period.

It was decided to investigate this problem in greater detail, and batches of bees were marked individually on 21 and 30 July. From 23 July onwards the poppy flowers were inspected each morning from 07.00 hr. until at least 08.00 hr., and records made of all marked bees seen. The following results were obtained:

(*a*) Forty-eight bees from Shirley poppies marked individually on 21 July.

23 July (3rd day): 35 (73 %) still on Shirley poppies; 1 on *Limnanthes* only.

24 July (4th day): 29 (60 %) still on Shirley poppies; 1 on *Limnanthes* only.

25 July (5th day): 18 (37 %) still on Shirley poppies; 1 also on *Nemophila* and 1 also on *Limnanthes*; 1 on *Limnanthes* only.

26 July (6th day): 7 (15 %) still on Shirley poppies; 1 also on *Nemophila*; 1 on *Limnanthes* only.

29 July (9th day): 1 (2 %) still on Shirley poppies; and also on *Limnanthes*.

31 July (11th day): none on Shirley poppies; but 1 on *Limnanthes* only.

(*b*) Twenty-seven bees from Shirley poppies marked individually on 30 July.

31 July (2nd day): 17 (63 %) still on Shirley poppies, 1 also on *Limnanthes*.

1 August (3rd day): 14 (52 %) still on Shirley poppies; 1 also on *Limnanthes*.

2 August (4th day): 10 (37 %) still on Shirley poppies; 1 on *Limnanthes* only.

5 August (7th day): 1 (4 %) still on Shirley poppies; (*Limnanthes* now over).

6 August (8th day): 2 (8 %) still on Shirley poppies.

7 August (9th day): 1 (4 %) still on Shirley poppies.

8 August (10th day): 1 (4 %) still on Shirley poppies.

On 6 August a search for marked bees was made on the combs of several nearby colonies, and eight of these 75 marked bees were found. None of these had been observed in the garden more recently than 2 August, and one had not been seen since 24 July. These bees had almost certainly switched to crops elsewhere, and their companions had probably done likewise.

A substantial proportion of the marked bees was found on the first day of observation after marking, and this affords evidence that the technique of marking was satisfactory and that most of the bees marked were at that time attached to this foraging area, and not merely random wanderers to it. The data are insufficient to enable a precise estimate of period of attachment to be made, but the rate of decrease indicates that the average period of attachment was not more than 8 days, although one of the first batch was noted on the 9th day, and one of the second batch on the 10th day. The longest record of attachment to these Shirley poppies was actually provided by a bee which was marked on 14 July and regularly seen until the 11th day, 24 July.

Less detailed results from other pollen-yielding plants also indicate a short period of attachment. Thus of 15 bees marked individually on nasturtiums, of which 13 were present 2 days after marking, only two persisted until 9 days after marking. Thirty-five bees were marked on *Eschscholtzia* on 7 July, and the last one was seen on these plants on 18 July. This last record indicates persistence for 12 days, and was the longest period of attachment to a purely pollen source.

Different results were obtained from bees marked on *Limnanthes*, which yields nectar as well as pollen. Three bees which had been marked on *Eschscholtzia* on 7 July were observed working on *Limnanthes* on 12 July, and on this same day seven more bees, then working on *Limnanthes*, were marked. Of the three which had switched from *Eschscholtzia* to *Limnanthes* one was regularly working on *Limnanthes* until 31 July, and so had been working in the garden for 25 days, and on *Limnanthes* for at least 20 days. One of the seven bees marked on 12 July worked regularly on *Limnanthes* until 1 August, or for at least 21 days.

The full results of these observations are that two out of 10 marked bees which worked *Limnanthes*, a source of nectar and pollen, remained on this plant for 20–21 days; from 136 bees marked on Shirley poppies, *Eschscholtzia* and nasturtiums, plants which are very attractive to bees but yield only pollen, the longest recorded attachments were 12 days (once), 11 days (once), 10 days (once), 9 days (three times).

Examination of the methods of bees when working nasturtiums introduced a related problem. Between 4 and 6 August all of the 13 bees which were working upon nasturtiums were marked, and from 5 to 8 August the nasturtium plants were examined at

intervals during both morning and afternoon, and the bees on them were recorded. The results, which are presented in Table 4, showed that two of the bees consistently worked the nasturtiums throughout the day, that two others were paying regular morning visits but were not always present in the afternoon, and that eight were present only in the mornings. The results of an all-day watch of the bee *C* (Table 1) showed no indication of any deterioration in the pollen yield during the day, and I therefore conclude that the bees which were working the nasturtiums ated from dual working. In several instances, as already recorded, a bee worked two crops at once, and others would regularly work on a pollen plant until their chosen nectar plant began to yield, deserting the former for the latter as soon as possible.) Most of the changes were simple, but one bee changed from *Eschscholtzia* to both Shirley poppies and *Limnanthes*, and another (*E*) from nasturtiums to *Eschscholtzia* and *Limnanthes* and then to Shirley poppies and *Nemophila*. These instances are represented by the divided arrows.

Table 4. *Foraging periods of* 13 *bees attached to nasturtiums*

	Present all afternoons		Present some afternoons		Present in mornings only								
Date and time	i	ii	iii	iv	v	vi	vii	viii	ix	x	xi	xii	xiii
5 Aug. morning	+	.	.	+	+	.	.	.	.	.	.	.	.
afternoon	+	.	.	−	−	.	.	.	.	.	.	.	.
6 Aug. morning	+	+	+	+	+	+	+	.	.	.	.	.	.
afternoon	+	+	+	+	−	−	−	.	.	.	.	.	.
7 Aug. morning	+	+	+	+	+	+	+	+	+	+	+	+	+
afternoon	+	+	+	−	−	−	−	−	−	−	−	−	−
8 Aug. morning	+	+	+	+	+	+	+	+	+	+	+	+	+
afternoon	+	+	−	+	−	−	−	−	−	−	−	−	−

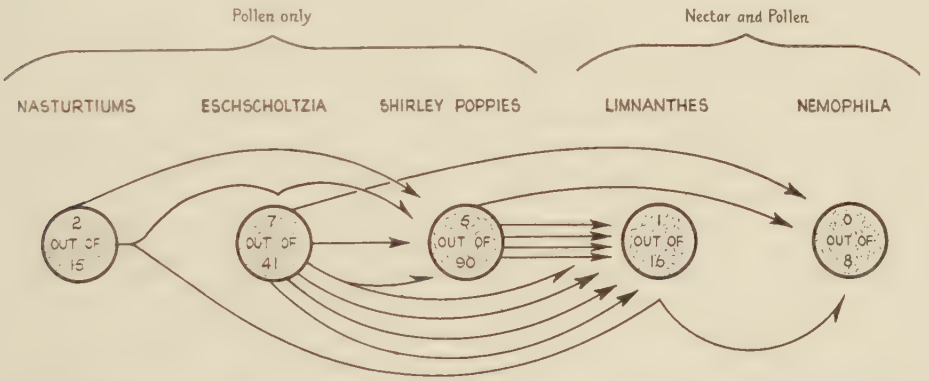


Fig. 9. Examples of change of crop. Each arrow or divided arrow represents one bee. Numbers in circles correspond to the number of changes and total number of marked bees which visited each crop.

during the mornings only were attracted away in the afternoon by better crops, probably nectar crops, then available elsewhere.

(*d*) *Examples of change of crop*

The observed changes of crop are represented diagrammatically in Fig. 9. Each instance involved a complete switch over from one crop to another one. (These complete switches must be clearly differenti-

The diagram emphasizes the important point that the changes were in one direction only. Comparison of the order of the changes among the three pollen plants indicates that they are in accord with the order of attractiveness as indicated by the foraging statistics. The latter showed that the nasturtium forager *C* visited 117 blossoms per trip, of which 54% were unfruitful, the *Eschscholtzia* foragers visited from 16 to 80 blossoms per trip, of which 54% were unfruitful, and the four Shirley poppy foragers visited from 1 to

20 blossoms per trip, all fruitful. A bee changed from nasturtiums to *Eschscholtzia*, but not vice versa, and no bee was ever seen to leave Shirley poppies, on which there were the largest numbers of marked bees, for either *Eschscholtzia* or nasturtiums.

The directional nature of the changes provides evidence of the relative attraction of pollen and nectar; nectar crops were preferred to pollen crops although they took up to twenty times as long as pollen loads to collect.

About 10% of the bees working the pollen crops were seen to switch to other plants in the garden. When the very limited choice available to the bee is taken into consideration this percentage does not seem very low, and I think that it may be taken as an indication that when the chosen forage plant of a bee becomes unsatisfactory she has a tendency to search for alternatives in that vicinity before going off elsewhere.

(*e*) *Effect of weather on time of collection of Shirley poppy pollen*

The pollen of the Shirley poppy flowers all became available when they opened early in the morning, usually by 06.30 hr. The flowers were very attractive to bees, three or four of which were sometimes visiting one blossom at once. The flowers were usually cleared of all their pollen within a few hours. There was great variation in the pollen yield of different blossoms, and later in the season the flowers were smaller and their yield less.

The number of bees foraging on the poppies was counted at half hourly intervals on 14 mornings between 16 July and 8 August. Peak populations were usually observed (eight times) at 08.00 hr., but sometimes at 07.00 or 07.30 hr., and all the bees had usually deserted these flowers by 10.00 hr. A typical record was that of 1 August, as follows: 07.00 hr. 52 bees, 07.30 hr. 67 bees, 08.00 hr. 70 bees, 08.30 hr. 51 bees, 09.00 hr. 22 bees, 09.30 hr. 21 bees, 10.00 hr. 1 bee.

But on two mornings the weather was unsuitable for flying, and the foraging records were very different. On 17 July there was rain until 09.30 hr., and the rest of the day was sunless and sultry. The record was: 09.00 hr. 0 bees, 09.30 hr. 0 bees, 10.00 hr. 15 bees, 11.00 hr. 33 bees, 12.00 hr. 29 bees, 13.00 hr. 14 bees, 14.00 hr. 13 bees, 14.30 hr. 9 bees.

On 5 August the temperature at 09.00 hr. was only 60° F. (previous days 67–69°) and there was no sunshine until after 10.00 hr.

The counts were: 07.00 hr. 13 bees, 07.30 hr. 14 bees, 08.00 hr. 2 bees, 08.30 hr. 12 bees, 09.30 hr. 14 bees, 10.30 hr. 24 bees, 11.00 hr. 16 bees, 12.30 hr. 1 bee.

On the days when flying conditions were least suitable the flighting of the bees was delayed, and fewer bees visited the blossoms, but this was compensated for by the longer foraging period, and foraging still continued until all the pollen had been harvested.

Honey-bees have been shown to have a very accurate time-sense (Beling, 1930), but on 17 July, when there was no flighting during the usual time for pollen-gathering, they came along at a later time.

The bees which came at this later time included marked bees whose known habit was to leave for other crops, but it should be pointed out that the bad weather had probably made these alternative crops unsuitable.

4. CONCLUSIONS

(*a*) *The behaviour of the individual honey-bee when foraging*

Bonnier (1906) one day marked all the bees working on a 3 × 16 ft. strip of buckwheat, and next day he found only marked bees there. Minderhoud (1931) made field studies of the area ranged over by bees working on clover, dandelion and other plants, marking all bees on areas of 1 sq.m. and then noting their movements on squared paper. He found that they returned to the same square, or within a radius of 10 yd. Buzzard (1936) marked a dozen bees out of about a hundred working upon three bushes of *Cotoneaster horizontalis*, each bush covering an area approximately 2 yd. square. He made fifteen observations during the next 5 days and found that the same bees returned to the same bush, and strayed only where the branches intertwined. Three strayings were observed, in each case followed by almost immediate return.

Butler, Jeffree & Kalmus (1943) marked about 100 bees working on a 5 × 8 yd. patch of willow herb (*Epilobium angustifolium*) situated in the middle of a larger area, and found that within 24 hr. these bees seldom moved more than 5 yd. beyond this patch. They also marked bees foraging upon three patches of globe thistle (*Echinops sphaerocephalus*) situated 18 yd. apart, and found that the proportion straying from patch to patch was about 10% per day. Then they conducted experiments using Petri dish feeders filled with syrup, and found that if such a source was kept full individuals would return again and again to the same dish. Bees searched for and found dishes farther afield only if their first supply failed. As a result of such failures they could become accustomed to foraging from several dishes, and in such circumstances they would then choose the dishes with the more concentrated syrup, if two kinds were offered at once.

My results provide further demonstration of the existence of definite foraging areas, and they indicate

in addition that the size of the foraging area may be very variable. One example has been given showing temporary attachment to an area in the immediate vicinity of one blossom, and another of attachment which ranged over the length and breadth of the experimental garden. The chief factors affecting the size of the foraging area are probably the number of flowers available, their nectar and pollen content, together with the amount of competition provided by other foragers.

I consider that the attachment to foraging areas is a consequence of the method used when foraging, and that, like the other features of the foraging behaviour, it can be considered a consequence of the exercise of choice and memory.

When a bee visits a good source of supply she tends to remain upon it; after an unsatisfactory visit she tends to turn elsewhere. The extent of her tendency to change is determined by her memory of past yields. When a crop becomes unsuitable and is deserted in favour of another the bee continues to return, although less and less often, to inspect the original source, but this is likely to occur only if the original source is remembered as having been superior to the new source. This pattern is shown most clearly by *E*, while working *Eschscholtzia* and *Limnanthes* together; other examples are the behaviour of *D*, which worked Shirley poppies and *Limnanthes* at different times of the day, and inspected the latter while working upon the former (but never vice versa), and the behaviour of *B*, which returned regularly to one favourite blossom.

There is a similar explanation for another feature of foraging behaviour, which was exemplified by *A*, while working upon *Eschscholtzia*. Her foraging visits were not distributed randomly within her foraging area; instead she showed a marked preference for different portions of it at different times of the day. I attribute this to a tendency to return to whatever portion of her foraging area she found most satisfactory, to work this more frequently until it was worked out, and then to select another portion. The bee *B*, working upon Shirley poppies, illustrated how by an extension of this method she could gradually change her foraging area: on 23 July, for instance, her visits were concentrated upon square B, which was outside the limits of her foraging area of a few days previously.

Another example of foraging behaviour may at first appear contrary to the exercise of choice. The forager upon nasturtiums displayed a pronounced tendency to return to square L, which was not apparently superior to other squares visited by her. The origin of this centripetal tendency can probably be seen in the behaviour of *B*, when she returned again and again to one individual flower. This flower was at first superior to neighbouring ones, and the bee remembered this and returned even when the superiority had disappeared. By an extension of this concept the centripetal tendency can be explained as an expression of the exercise of choice and memory, instead of a contradictory phenomenon. The centripetal tendency is perhaps likely to be more characteristic of nectar gatherers than pollen gatherers, because nectar supplies are more usually replenished than pollen ones. A characteristic of this behaviour pattern was that the centripetal tendency was much more pronounced in relation to initial visits than to the other ones.

During the present series of observations careful attention was paid to both the starting- and finishing-points of foraging trips. In most cases the starts of a series of trips were scattered throughout the foraging area, and the trips were finished, usually without an orientation flight, at any spot where the bee happened to complete her load. However, in the two instances in which the centripetal tendency was most marked this led to the *commencement* of most of the trips either on one small patch of nasturtiums or, in the extreme example, on a single blossom of Shirley poppy. There was no evidence of a similar concentration of last visits, which were apparently random, and the explanation which I have given for the concentration of the initial visits would not suffice to explain a similar concentration of last visits, if such had been observed. These observations are only in partial agreement with the statement of Butler (1945) that a bee working a particular foraging area 'almost always' alights first on one particular plant, and that after moving elsewhere in the area she eventually returns to the flower first visited and takes off from it on her return flight to the hive.

A characteristic of bees working upon failing sources was that they became more restless and questive, so that instead of visiting flowers quite close to each other they jumped from one portion of their usual foraging area to another, and even beyond it. This trait was noted in *A* when working *Eschscholtzia* while their blossoms were closing, and in bees working upon Shirley poppies the pollen supply of which was becoming exhausted. It was also observed in one of the two bees which worked *Limnanthes* for a long period; this bee worked only upon this crop from 12 July until 1 August (by which time there were so few flowers left on it that it no longer provided suitable forage) except on 31 July when she was observed for the first and only time to visit a few blossoms of *Nemophila* on squares F and G.

Some blossoms were much more attractive than others, and among *Eschscholtzia* and Shirley poppies this was obviously associated with the quantity of pollen available. Bees made no apparent distinction between flowers which had been recently visited (either by other bees or by themselves) and those

which had not, and pollen gathering often involved repeated visits to selected blossoms, sometimes on the same trip, just as nectar gathering does (Butler, 1945). This conclusion runs counter to the suggestion of Park (1947) that bees can recognize on flowers the scent left by previous visitors, and avoid these flowers.

When a portion of her foraging area became shaded the bee *A* worked upon both shaded and unshaded flowers without discrimination; this observation makes interesting comparison with the conclusive evidence provided by Butler *et al.* (1943) that the number of bees attracted to dishes of syrup placed in shade was only a small proportion of the number attracted to similar unshaded dishes.

A few examples are given of bees which were seen to work two different crops in the garden at different times of the day. It was also observed that nasturtiums provided a satisfactory pollen supply throughout the day, but two-thirds of their foraging population worked only in the mornings (Table 4). This convinces me that most of these bees, together with those whose only garden visits were morning ones to Shirley poppies, were foraging elsewhere, probably on nectar crops, during the rest of the day. Such dual working would be facilitated by the accurate time sense which bees are known to possess (Beling, 1930). The value of this time sense can be seen by comparing the behaviour of the bee *D*, which had worked both Shirley poppies and *Limnanthes* for several days, with the behaviour of *E*, which worked Shirley poppies and *Nemophila*, without having previously been on the former crop. *D* did not alight to inspect *Limnanthes* during any of her first seven observed trips, but *E* inspected the *Nemophila* before visiting the poppies, and at frequent intervals thereafter. Although the time sense is helpful to the bee, her timetable is not inflexible, for after wet mornings marked bees came to Shirley poppies in the afternoon, commencing foraging after their usual finishing time.

It has been generally recognized that honey-bees usually confine their attention to one plant only on any one foraging trip, and frequently this constancy has been exaggerated. The most extensive work is that of Betts (1935), who analysed 915 pollen loads, of which 18 were mingled mixtures and seven were segregated mixtures—a total of 3% mixtures. She also observed that an additional 15% of the loads contained a few different grains. She thought that propinquity was more important than plant characteristics in determining whether loads would be mixed. The present observations confirm this view, and show that mixed loads are not necessarily brought in only by unattached bees, but that in suitable circumstances a bee can become attached to and forage from two very different crops at one time.

The changes of crops now recorded have been found to be directional, and in accord with the order of attractiveness as indicated by the foraging statistics, Shirley poppies being preferred to *Eschscholtzia* and the latter to nasturtiums. The relative attractiveness of these three crops was probably consistent, but this is less likely to be true of nectar-yielding crops. If the order of attractiveness of such crops varies (e.g. with climatic changes) some bees will probably be found to make reversible changes in attachments, making use of their power of inspection of past crops.

(*b*) *The basic principle of foraging behaviour*

Butler (1945) followed his earlier observations with a theory of foraging behaviour. He said that the foraging population consists of 'scout' bees, 'wandering' bees, and 'fixed' bees, the 'scout' bees being young ones which leave the hive without any preconceived foraging ideas, the 'wandering' bees those which seek flowers the scent of which has been communicated to them within the hive by successful foragers, and the 'fixed' bees those confining their attention to a small 'fixation area', some 4–5 yd. in diameter, of a particular crop, where they stay either until they die or until the crop fails. He suggested that the 'scout' and 'wandering' bees would 'fix' in any area from which they could obtain a full load of nectar within 30–60 min.

This theory implies that foraging behaviour is rigid and automatic, and perhaps based upon a simple total reflex. Yet the observations of Butler *et al.* (1943) on the behaviour of bees when the syrup in dishes upon which they had been foraging began to dry up are difficult to explain in such terms, and so are those of von Frisch (1934), who had found that the concentration of syrup required to keep bees visiting dishes varied in almost every experiment, depending apparently upon the concentration of syrup upon which the bees had last fed, and also that the lowest concentration varied not merely between one individual and another, but also in any one individual from time to time.

My observations of bees working upon natural crops agree with these observations of variable behaviour upon dishes. From them I conclude that foraging behaviour is not fixed, but adaptable. I therefore use the term 'attach' instead of 'fix', and speak of 'foraging areas' instead of 'fixation areas'.

I think that the basic and cardinal feature of the foraging behaviour is the continuous exercise of choice and the comparison of the present with memories of the past, and that it is the resultant of these factors which determines whether the bee will remain attached to any particular crop and area. The present results have illustrated how a bee can use choice and memory in order to select the most suitable blossoms of the crop which is being worked, when

showing a preference for different portions of her foraging area at different times, in order to produce a gradual change in the position of her foraging area, when working one crop and inspecting another, when working two crops at once, when working two crops at different times of the day, when crops are failing, and when changing crops.

I consider that attached bees are satisfied ones. Gradations of observed behaviour can be explained by supposing that there is no absolute criterion of satisfaction but a continuous gradation between complete satisfaction (Butler's 'fixed' bee) and complete dissatisfaction (Butler's 'scout' bee, except that there is no evidence that such bees are necessarily young ones).

On any crop we may expect to find a considerable range of observed behaviour resulting from a similar range of satisfaction, because the state of satisfaction of an individual will vary with the previous experience of that individual, and her inherited make-up, as well as with the state of the crop which she is working.

(*c*) *The circumstances in which bees change from crop to crop*

The 'fixation' theory of foraging behaviour supposed that 'fixed' bees would change their crops only when those crops failed, but the numerous changes of crop which are now recorded always involved desertion from a crop which was still being worked satisfactorily by other bees; in most instances newcomers were still being attracted to the forsaken crop.

I conclude from my results that change of foraging area and crop is often not an infrequent phenomenon. It is important to recognize that the world of a bee is a very inconstant one; she has to forage in a very variable climate, and on crops whose nectar abundance and concentration varies very greatly from day to day and from hour to hour. In such circumstances it must be expected that there will be frequent occasions when her chosen crop temporarily deteriorates, and so provides a stimulus for her to move to a better one, if she can find it. There is no evidence which will enable us to decide whether crop changes are always a consequence of dissatisfaction with the forsaken crop, but there is at least a possibility that a better crop in the vicinity of a satisfactory one may occasionally be found as the result of curiosity, or that a good crop may be deserted in favour of a better crop elsewhere as a result of a communication received within the hive from a more successful forager. The regular desertions from the excellent pollen crops provided by Shirley poppy indicate that factors within the bee may play a part in the forsaking of crops which yield pollen only.

One may expect that the proportion of bees changing their foraging areas will vary greatly with local circumstances such as the disposition of crops and the quantity of nectar and pollen available in them, so that one set of observations may indicate a high proportion of changes, and another set a low one. This variation would explain the conflict of views on this matter among observers of bee behaviour. The results now published provide an example of one bee which changed its foraging area at short intervals, and of another bee which was attached for at least 21 days. This latter is the longest period of attachment yet recorded—4 days longer than the 17-day attachment recorded on willow herb by Butler *et al.* (1943).

We know nothing of how bees find crops on their first foraging trips, but it is reasonable to suppose that there is an inborn behaviour predisposition which can help them to find suitable nectar and pollen sources in the first place, because we know that nuclei consisting of newly emerged bees only can perform a normal sequence of hive duties, and then go foraging (Wiltze, 1882; Nelson, 1927). This does not preclude the possibility that these first trips may sometimes follow directions obtained from the dances of successful foragers (von Frisch, 1946).

5. SUMMARY

Honey-bees foraging in a specially planted flower garden were chloroformed and given individual marks. Their movements were then recorded from day to day, and a few selected bees were watched continuously for periods of a day or more. It was concluded that:

1. The basic principle underlying the foraging behaviour pattern is the continuous exercise of choice by the bee, which chooses the best portions of the best of any alternative crops with which she becomes acquainted, and compares present crops with her memory of past crops.

2. Bees usually attach themselves to a particular area of the most suitable crop found. The size of this foraging area varies considerably.

3. Examples are given of the use of choice and memory in order to select the most suitable blossoms of the crop which is being worked, when showing a preference for different portions of a foraging area at different times, in order gradually to change the position of a foraging area, when a bee is working one crop and inspecting another, when she is working two crops at once, when she is working two crops at different times of the day, when crops are failing, and when changing crops. The centripetal tendency shown by some foragers is considered to be a consequence of the interplay of choice and memory.

4. Attachment may be of any duration, from a few trips to a lifetime. The proportion of changes of attachment may be expected to vary greatly with local

circumstances, because behaviour is labile and readily adaptable to changing conditions.

5. Bees which became attached to sources yielding pollen without nectar remained for only a part of their foraging life. Bees were frequently seen to change their attachment from a pollen crop to a nectar crop, but never vice versa.

6. Nectar gatherers were observed to make from 250 to 1446 flower visits per load, and from about 300 to 1000 flower visits per foraging hour. Pollen gatherers averaged from 7 to 120 flower visits per load, and from about 50 to 150 fruitful flower visits per foraging hour. These limits may possibly be widely exceeded in other circumstances. Such statistics are not an index of the pollinating capacity of the bee, as foraging is often mainly composed of oft-repeated visits to favourite blossoms. The size of foraging area is a more correct index of pollinating capacity.

6. ACKNOWLEDGEMENTS

I am indebted to Dr C. G. Butler, Head of the Bee Research Department at Rothamsted, for the facilities for this work and for stimulating criticisms during its progress, and to Mr M. J. R. Healy, of the Statistical Department at Rothamsted, for calculations of significance tests.

REFERENCES

Beling, I. (1930). 'Über das Zeitgedächtnis der Bienen.' Naturwissenschaften, 18: 63–7.

Betts, A. D. (1935). 'The constancy of the pollen-collecting bee.' Bee World, 16: 111–13.

Bonnier, G. (1906). 'Sur la division du travail chez les abeilles.' C.R. Acad. Sci., Paris, 143: 941–6.

Butler, C. G., Jeffree, E. P. & Kalmus, H. (1943). 'The behaviour of a population of honeybees on an artificial and on a natural crop.' J. Exp. Biol. 20: 65–73.

Butler, C. G. (1945). 'The behaviour of bees when foraging.' J. R. Soc. Arts, 93: 501–11.

Buzzard, C. N. (1936). 'De l'organisation du travail chez les abeilles.' Bull. Soc. Apic. Alpes-Marit. 15: 65–70.

Frisch, K. von (1944). 'Über den Geschmackssinn der Biene. Ein Beitrag zur vergleichenden Physiologie des Geschmacks.' Z. Vergl. Physiol. 21: 1–156.

Frisch, K. von (1946). 'Die Tänze der Bienen.' Osterr. Zoolog. Z. 1: 1–48. [English translation in 1947, Bull. Anim. Behav. 1 (5): 32 pp.]

Himmer, —. (1930). Quoted by Betts, A. D. in Amer. Bee J. 70: 447.

Minderhoud, A. (1931). 'Untersuchungen ueber das Betragen Honigbiene als Blutenstauberin.' Gartenbauwiss. 4: 342–62.

Nelson, F. C. (1927). 'Adaptability of young bees under adverse conditions.' Amer. Bee J. 67: 242–3.

Park, O. W. (1928). 'Time factors in relation to the acquisition of food by the honeybee.' Res. Bull. Ia Agric. Exp. Sta. 108: 184–225.

Park, O. W. (1947). 'Activities of honeybees.' In Grout, R. C. 'The hive and the honeybee.' London, pp. 125–206.

Vansell, G. H. (1942). 'Factors affecting the usefulness of honey-bees in pollination.' Circ. U.S. Dep. Agric. 650: 31 pp.

Wiltze, J. (1882). 'Work done by two quarts of bees before 16 days old.' Glean. Bee Cult. 10: 596–7.

AN ECOLOGICAL STUDY OF THE RIVER RHEIDOL, NORTH CARDIGANSHIRE, WALES

By J. R. ERICHSEN JONES
Department of Zoology, University College of Wales, Aberystwyth

(With Plates 1–3 and 7 Figures in the Text)

CONTENTS

	PAGE
1. Introduction	67
2. The environment	67
(*a*) General topography	67
(*b*) The regions examined in the present survey	69
(*c*) Current, hydrogen-ion concentration, temperature, oxygen	70
(*d*) Chemical	77
3. The flora	78
4. The fauna	79
(*a*) The species recorded	79
(*b*) Remarks on the fauna	84
5. Summary	87
References	87

1. INTRODUCTION

The River Rheidol has been the subject of considerable study in the last 29 years, for it presents an interesting example of a river which has slowly recovered from lead pollution. When Carpenter (1924) began her study of the river in 1919, the once prosperous lead-mining industry of Cardiganshire was in its final stages of decline but the river was still heavily polluted, supporting a very scanty algal and bryophyte flora and a fauna limited to some fourteen species, all Arthropoda. In 1922, after all lead-mining operations in the valley had come to an end, the recovery of the river began; by March 1923 the fauna list included 29 species, the algal and bryophyte flora was considerably improved and some phanerogamic vegetation had become established. At this point Carpenter's records for the Rheidol cease, but later (1927) in a general study of the ecology of Cardiganshire streams 57 species are named in a combined list for the rivers Rheidol and Ystwyth.

The next study of the river is the faunistic survey of Laurie & Jones (1938). This work was based on collections carried out in its lower reaches from July 1931 to May 1932, and a further examination of the same regions in the autumn of 1936. In this survey a great improvement in the fauna became evident, for about 103 animal species were recorded and it was shown that lead pollution had diminished to negligible proportions. Since this survey the improvement in the river's condition has been maintained, there has been no renewal of pollution and its lower reaches have been successfully stocked with trout.

In the autumn of 1947 the writer again took up the study of the river. This resumed investigation was prompted by a number of considerations; quite apart from the possibility of recording further improvement in the fauna it was felt that a more complete ecological study including the whole river would be of some value, for the Rheidol is a river of very interesting type, including a very wide range of habitat, and previous investigations have been practically confined to its lower course, the only biological work on its upper and middle reaches being Reese's study (1937) of its microflora. Furthermore, it is obvious that earlier investigations suffered somewhat from the lack of an adequate basis of comparison, for at the time they were carried out there had been practically no intensive ecological study of unpolluted rivers of similar type in Wales, whereas now the writer's studies of the rivers Dovey and Teifi (Jones, 1941, 1943) supply a more adequate background. Finally, the proximity of the river to the writer's laboratory at Aberystwyth has rendered possible a more complete physiographical study than could be attempted in the case of rivers too far away for frequent examination.

2. THE ENVIRONMENT

(*a*) *General topography* (Fig. 1)

The general topography of the river has been described in earlier studies (Carpenter, 1924, p. 1; Reese, 1937, p. 388; Laurie & Jones, 1938, pp. 272–3) and here it will be sufficient to recapitulate. The Rheidol has its source in Llyn Llygad Rheidol near the summit of Plynlimmon and its main-stream is divided into two roughly equal halves, the one flowing

Fig. 1. Map of the River Rheidol and its tributaries, showing the relief of the land and the position of the collecting stations A, B, C, D and E. S is the source of the river at Llyn Llygad Rheidol. The arrows indicating the Penybont area span the section of the river for which the current speed, temperature, oxygen and pH records were compiled.

Photo 1. The river entering the gorge, one mile below Ponterwyd.

Photo 2. The opening of the gorge above the Cwm Rheidol mine.

Photo 3. The cascades immediately below the Cwm Rheidol mine.

south to Devil's Bridge, the other westwards to Aberystwyth on Cardigan Bay. In Fig. 2 the profile of the river and some of its chief tributaries is drawn; this shows that the gradient of the river bed is generally steep, but very variable. In all the river falls 1750 ft. in about 28 miles, an average of nearly 63 ft./mile which is over twice the average fall for the River Tees (30 ft./mile—Butcher, Longwell & Pentelow, 1937, p. 1), one of the fastest rivers in England. A most important feature of the Rheidol, indicated in Fig. 1, is that it draws nearly all its water from land over 1000 ft. Here the mean annual rainfall is over 60 in. Its highland head-waters and tributaries are bounded by extensive peat bogs and moors characterized by *Sphagnum*, *Drosera rotundifolia*, *Carex* and *Lycopodium* (Reese, 1937, p. 388), and the soil of these regions is thin and very lacking in lime. Consequently the river is liable to frequent and violent floods and its water is always acid. In its lower course the river receives very few tributaries, the only one of any size being the Melindwr, which also draws almost the whole of its water from the lakes Syfydrin and Castell-coch situated just above 1000 ft. Consequently, at station B, above Ponterwyd, the stream normally has a flow of water which is practically equal to that at Aberystwyth, and chemically, and to some extent physically, the river retains its mountain character until it reaches the sea.

The lead-mining activities of the nineteenth century involved the crushing and washing of enormous quantities of stony material, and when the ore had been extracted the earthy impurities and quantities of rock too poor in ore to be worth crushing were cast into the river or heaped upon its banks to be carried away by floods. This accounts for the fact that in its final 10 miles the river is extensively silted up, shallow and erratic in course, with broad flood beaches of silt and rubble. The instability of its bed is probably one of the chief factors responsible for the river's lack of phanerogamic vegetation and Reese (1937, p. 392) has shown that the gritty lead-mine material tends to impair the algal growth by smothering it and scouring it away at flood time.

(*b*) *The regions examined in the present survey*

The highest of the collecting stations selected (A) is situated at Nant-y-moch at an altitude of about 1050 ft. This region is remote and difficult of access, but is of exceptional interest in that it lies above all the lead-mine workings and it is safe to assume that here there has never been any degree of pollution. Here the valley is open and treeless, sheltered by high hills from north and east winds, its floor is wide and flat and the river though only 3 miles from its source is already a fine, broad stream about 50 ft. from bank to bank. Its gradient is about 60 ft./mile, the bed remarkably flat and composed of large flat stones, pebbles and coarse gravel. At normal level the stream is shallow, about a foot deep in midstream, and flows comparatively gently.

The second collecting station (B) is situated about 2 miles above the village of Ponterwyd. This is one of the regions selected by Reese (1937) for her study of the microflora. Here the valley is still barren and treeless, its sides sloping very steeply to the river's banks so that the stream is confined to a constant course. The river presents, in some respects, a

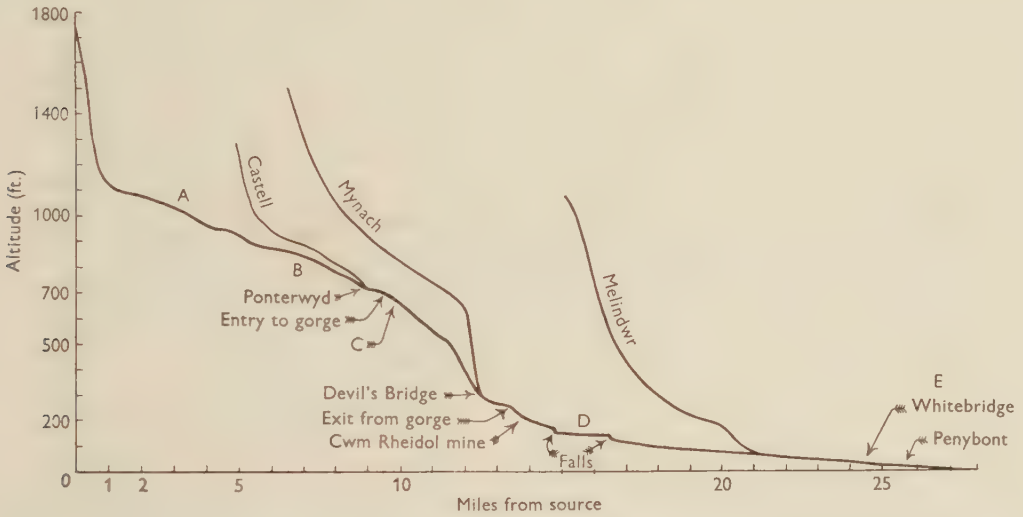


Fig. 2. The profile of the main-stream of the Rheidol and its chief tributaries.

gigantic edition of the cascade-reach of a mountain stream, for it is 80–100 ft. wide, carries a considerable volume of water, and consists of a series of long, deep, tarn-like pools connected by shallow rapids. The pools are 200–300 ft. long, the full width of the river, and at normal level are almost stagnant; they are bottomed by stones and much sandy debris sheltering numerous tube-building Chironomidae. When examined in October 1947 they contained great numbers of the Cladoceran *Eurycercus lamellatus*. The rapids are in great part rocky, the bed extremely irregular, and in crevices in the rocks large, weathered stones are lodged; elsewhere the stream-bed is composed of boulders, stones and pebbles, and here and there, where the current is more gentle, there are little beaches of sand and gravel where silt may be deposited in the intervals between floods. In this region collecting is difficult, even when the level of the river is low, owing to the irregularity of the bed, the swiftness of the current, and the luxuriance of the algal flora which renders the stream-bed extremely slimy.

A little farther to the south the river enters a gorge which is about 4 miles in length. Here the gradient of the stream-bed increases, eventually to nearly 200 ft. per mile, and the sides of the valley become steeper and steeper until the river becomes a narrow and deep torrent flowing at some points between almost vertical walls of rock. Station C, about a mile below Ponterwyd, is at the beginning of the gorge section; at this point the west bank of the river is inaccessible, but it is possible to climb down to the east bank where there are a number of small rock pools. At low level the main-stream is only about 10 ft. wide at some points, the pools nearby have little or no vegetation and are bottomed with stones and sand, but those a little farther from the flowing water, and on a higher level, have a rich algal and bryophyte flora. The main-stream appears almost barren of animal life except in a few places where stones and large pebbles are deposited and shelter a lithophilous fauna which is a decimated copy of that found at station B. When visited early in November 1947 the pools had a rich and varied fauna, but the existence of the animals in this habitat is precarious; after floods later in the month only a remnant of the fauna survived.

The river emerges from the gorge just above the Cwm Rheidol mine, one of the largest and most recently worked mines in its valley. Below the mine it pours over the larger of two waterfalls, the smaller is about 2 miles lower down the valley. These waterfalls have no fish passes and probably form impassable obstacles to migratory fish. Station D is located between the two falls, here the gradient of the river has slackened, and the main-stream has spread out to a width of 80–150 ft. Its bed is in some places rocky, in other places composed of large, flat stones and pebbles, with the addition of gravel and silt where the current is comparatively gentle. There are no backwaters as the valley is still narrow.

Below station D the valley widens, the river bed gradually becomes less rocky, and the stream meanders. In the lower reaches of the river no single locality is sufficiently representative and fauna samples were taken at Penybont, just above the tidal area, and at the 'Whitebridge', about a mile to the east. Fig. 3 is a large-scale map of the Whitebridge area; here the river is very silted up, shallow and erratic in course, with great flood beaches of rubble and silt reminiscent of the River Ystwyth (cf. Jones, 1940, fig. 2). Its bed is composed of stones, pebbles and gravel, the stones generally much smaller than at station D. Here collecting is easy when the level of the river is low, as the bed is comparatively flat and the stream so shallow that it can be forded at many places. There are a number of backwaters in this region, all of which were investigated when taking a fauna sample; they are more fully described in the legend to Fig. 3. The Penybont area has been fully described in the earlier survey (Laurie & Jones, 1938, p. 276).

The backwaters below Penybont bridge, one of the collecting stations of the earlier survey, were not included in the present investigation, for in recent years the river has thrown up an immense rubble flood beach at this point and moved its course some distance to the south with the result that these backwaters are now completely separated from the main-stream except at high floods.

(*c*) *Current, hydrogen-ion concentration, temperature, oxygen*

From 14 January to 5 March 1948 regular observations were made on the rate of flow of the water, its hydrogen-ion concentration and oxygen content, and the air and water temperature in the Penybont area. The data are set out in Figs. 4 and 5 and in Table 1. It will be seen that the records include a mild and wet period with the river in heavy flood and a sudden cold spell followed by warm and dry spring weather. The Penybont area is convenient for regular observation as the river is confined by high banks and readily accessible even at heavy floods. Above the bridge a 1000 ft. stretch of the river was measured out and the speed of the surface water estimated by timing the movement of floats in midstream. Various types of float were tried out; when the flow is comparatively gentle 4 in. white cardboard disks are excellent, as they are easily seen and floating flat on the surface are not disturbed by the wind; but this type of float is less successful in rough flood water when it may be submerged and trapped between stones. For measurements at flood time bottles containing sufficient water to make them float almost completely immersed (as used by Chandler, 1937) were generally employed.

For the oxygen and temperature determinations the usual type of sampling bottle was used, fitted with an inlet tube leading to the bottom and an outlet tube for the escape of air. The former was sufficiently wide to allow the insertion of a thermometer so that the temperature could be taken immediately after withdrawing the sample bottle from the water. The bottle was fitted with a heavily weighted brass cage and thrown into flowing water about 18 in. deep and far from any large clumps of water weed where it filled in about 20 sec. Samples for pH determinations were taken with a similar apparatus, the pH records are all colorimetric determinations with Chloro-phenol red, Bromo-cresol purple and Bromo-thymol blue. Air temperatures were taken in the shade of the bridge at Penybont.

All the observations recorded in Figs. 4 and 5 were made approximately at 14.00 hr. G.M.T. At this time the oxygen content of the water is near its maximum for the day, the air temperature is generally at its maximum during this season of the year and the water temperature, though not the maximum for the day, can be taken as representative (see the records for 11 February, Fig. 6 and Table 2).

At low level the river has a midstream velocity at Penybont of 1·3–1·5 ft./sec. and at full flood this may rise to nearly 6 ft./sec. These current speed differences correspond to a rise in level of about 2 ft. at Penybont bridge. This level difference may appear small, but for comparison it may be noted that a 2 ft. rise in the level of the Tees at Barnard Castle, about 30 miles from its source, corresponds to a rise in the total flow from 5 million cu.ft./12 hr. to 112 million cu.ft./12 hr. (Butcher *et al.* 1937, p. 16).

On the riffles in the Whitebridge area and at station D the speed of the current is considerable even when the level of the river is low; some observations made in May 1948 when the flow over the standard section at Penybont was 1·4 ft./sec. gave values of 4½–5 ft./sec. at the surface in midstream, where the water was 8–12 in. deep. These results were obtained by timing the movement of floats over 30 ft. lengths of the river bed marked out with stakes. The riffle current increases to about 6 ft./sec. when the river level is normal and it is probable that even more powerful currents develop when the river is in flood, but no satisfactory method of estimating their speed could be devised. It is not possible to wade in the river at flood time and the timing of floats over distances measured on the river bank is not satisfactory over short distances. It would appear, however, that at full flood the great bulk and momentum of the moving

Fig. 3. Large-scale map of the Whitebridge area; based on the ordnance survey, the course of the river checked in March 1948. F is the Whitebridge backwater, station B of the earlier survey by Laurie & Jones; it is now a cul-de-sac as its eastern entry has closed up. G, H and L are backwaters bottomed with muddy sand and with abundant phanerogamic vegetation; M is a shallow backwater with no macroflora and bottomed with stones and silt. Main-stream collections were made at N and between M and H. To the west of the road-bridge (centre of map) the river is changing its course. In 1947 it began to flow through the old mill-race P, previously a series of pools, and the floods of January and February 1948 deposited great quantities of rubble near L. By May 1948 backwater L was largely filled up, the bulk of the main-stream water was passing through the mill-race and the south bend of the river appears destined to become a backwater or cut-off.

water tends to establish a much more uniform current speed, particularly where the banks limit the lateral expansion of the stream.

0·1 m./sec. as 'very slight', 0·1–0·25 m./sec. as 'slight', 0·25–0·5 m./sec. as 'medium', 0·5–1·0 m./sec. as 'strong', and all currents over 1 m./sec. as

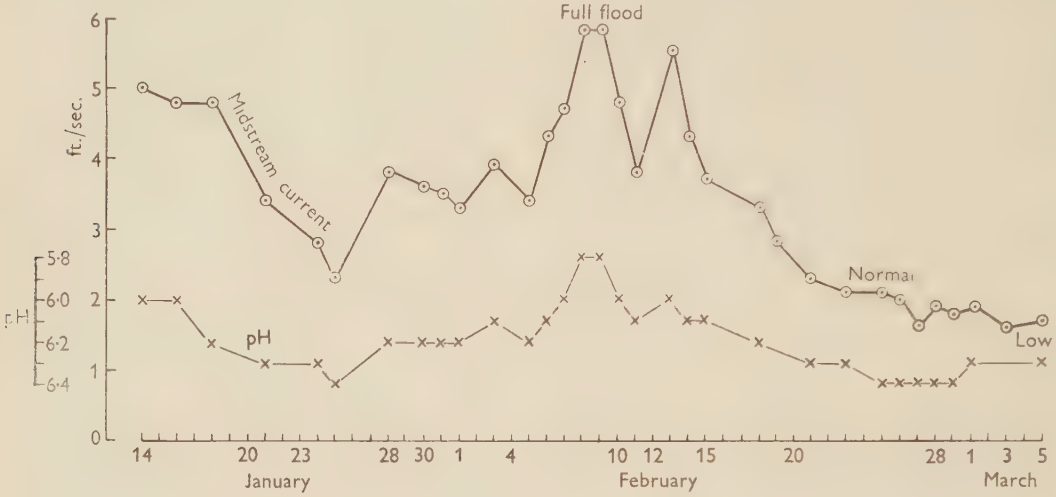


Fig. 4. Midstream current and pH records for the Penybont area 14 Jan.–5 March 1948.

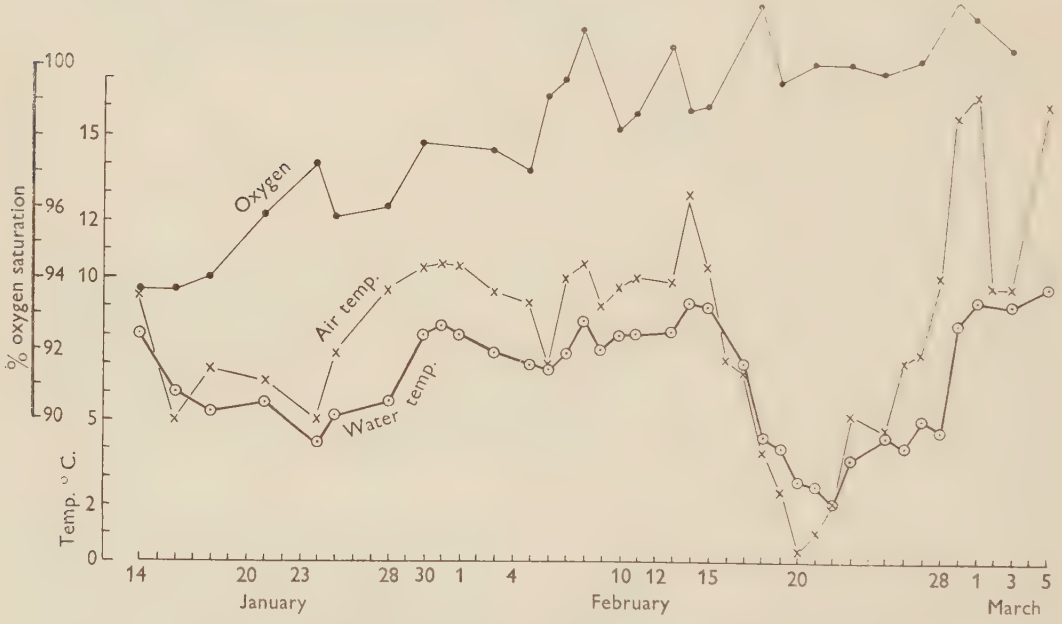


Fig. 5. Air and water temperature and percentage saturation of oxygen records for the main-stream in the Penybont area 14 Jan.–5 March 1948. Observations at 14.00 hr. G.M.T. approximately.

The current speed observations indicate that the Rheidol is a very swift river. Berg (1943, p. 54), discussing his data for current speeds in the Susaa and other Danish rivers, classifies currents of less than 'very strong'. Taking the metre as roughly 3·3 ft. it will be seen from Fig. 4 that in the Penybont area (where the non-tidal reaches of the river end) very strong currents may be maintained for considerable

periods; thus from 28 January to 18 February (21 days) the current speed did not fall below 1 m./sec. The maximum velocity of full flood, however, is not usually maintained for more than 2 or 3 days. In comparing the Rheidol with other rivers it may be noted that Southern & Gardiner (1938) state that the current speed of the Shannon between Lough Ree and Lough Derg is about 0·5 ft./sec. in summer and 5 ft./sec. in winter, while Butcher *et al.* (1937, p. 1) state that the average velocity of the Tees is 1½–2 miles/hr. (2·2–2·9 ft./sec.). Richardson (1921, p. 410) states that the average flood velocity of the Illinois river above Havana is about 0·9 miles/hr. (1·3 ft./sec.), but a speed of 229·47 ft./min. (3·8 ft./sec.) is recorded for the Morris to Utica section (Richardson, 1921, p. 377). Denham (1938) gives some interesting data for current speeds in White River, Indiana, in which the nature of the river bottom is correlated with the current; speeds of up to 0·55 ft./sec. are recorded for mud bottoms, up to 0·87 ft./sec. for mud and sand, and up to 2·29 ft./sec. for sand and gravel. The last is the highest current speed recorded for the riffles, but is presumably not a flood measurement.

Table 1. *Current speed*, pH, *air and water temperature, and percentage saturation of oxygen data for the River Rheidol at Penybont, 14 January to 5 March* 1948

Dashes indicate no determination

Date (1948)	Current (ft./sec.)	pH	Air (° C.)	Water (° C.)	Oxygen (% saturation)
14 Jan.	5·0	6·0	9·4	8·0	93·5
16	4·8	6·0	5·0	6·0	93·5
18	4·8	6·2	6·8	5·3	94·0
21	3·4	6·3	6·4	5·7	95·8
24	2·8	6·3	5·0	4·2	97·2
25	2·3	6·4	7·4	5·2	95·7
28	3·8	6·2	9·6	5·7	96·0
30	3·6	6·2	10·4	8·0	97·8
31	3·5	6·2	10·5	8·3	—
1 Feb.	3·3	6·2	10·4	8·0	—
3	3·9	6·1	9·5	7·4	97·6
5	3·4	6·2	9·2	7·0	97·0
6	4·3	6·1	7·0	6·9	99·1
7	4·7	6·0	10·0	7·3	99·6
8	5·8	5·8	10·5	8·5	101·0
9	5·8	5·8	9·0	7·5	—
10	4·8	6·0	9·7	8·0	98·2
11	3·8	6·1	10·0	8·0	98·6
13	5·5	6·0	9·9	8·1	100·5
14	4·3	6·1	13·0	9·1	98·7
15	3·7	6·1	10·4	9·0	98·8
16	—	—	7·2	—	—
17	—	—	6·7	7·0	—
18	3·3	6·2	3·9	4·4	101·7
19	2·8	—	2·5	4·0	99·5
20	—	—	0·4	2·8	—
21	2·3	6·3	1·0	2·7	100·0
22	—	—	2·0	2·0	—
23	2·1	6·3	5·2	3·6	100·0
25	2·1	6·4	4·7	4·4	99·8
26	2·0	6·4	7·0	4·0	—
27	1·6	6·4	7·3	5·0	100·1
28	1·9	6·4	10·0	4·6	—
29	1·8	6·4	15·6	8·4	101·8
1 Mar.	1·9	6·3	16·4	9·1	101·3
2	—	—	9·7	—	—
3	1·6	—	9·7	9·0	100·4
5	1·7	6·3	16·0	9·4	—

The pH records show that the water of the mainstream is always acid, the degree of acidity varying with the river level so that the pH swings from 6·4 at low level to 5·8 at full flood. This pH swing appears to

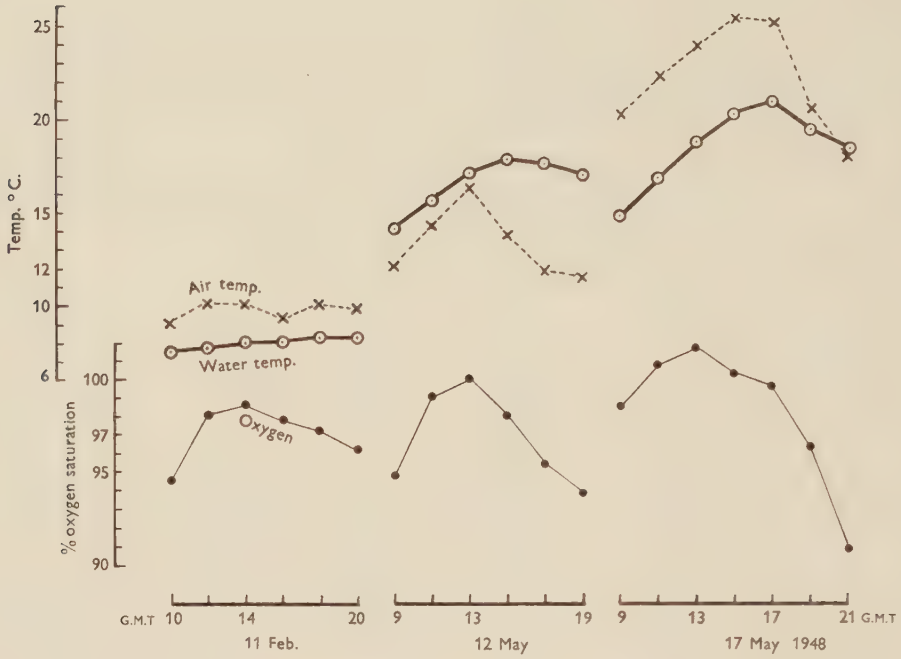


Fig. 6. Air temperature, water temperature and percentage saturation of oxygen records for the Penybont area on 11 February, 12 and 17 May.

Table 2. *Percentage saturation of oxygen, air and water temperature, current speed and* pH *data for the River Rheidol at Penybont on* 11 *February,* 12 *and* 17 *May* 1948

Date	G.M.T.	pH	Current (ft./sec.)	Water temp. (° C.)	Air temp. (° C.)	Oxygen (% saturation)	Weather
11 Feb.	10.00	6·1	—	7·5	9·0	94·6	Cloudy
	12.00	—	—	7·7	10·1	98·1	,,
	14.00	6·1	3·8	8·0	10·0	98·6	,,
	16.00	—	—	8·0	9·3	97·8	Heavy rain
	18.00	—	—	8·2	10·0	97·2	Light rain
	20.00	6·1	4·2	8·2	9·7	96·2	,,
12 May	09.00	6·4	1·4	14·0	12·0	94·8	Bright sun
	11.00	—	—	15·5	14·2	99·0	,,
	13.00	6·4	—	17·0	16·2	100·0	,,
	15.00	—	—	17·7	13·6	98·0	,,
	17.00	6·4	—	17·5	11·8	95·4	,,
	19.00	—	—	16·8	11·4	93·9	,,
17 May	09.00	—	—	14·7	20·0	98·4	Bright sun
	11.00	6·4	—	16·8	22·1	100·6	,,
	13.00	—	1·4	18·7	23·7	101·5	,,
	15.00	6·4	—	20·2	25·2	100·2	,,
	17.00	—	—	20·9	25·0	99·5	,,
	19.00	—	—	19·5	20·5	96·2	,,
	21.00	—	—	18·5	18·0	90·8	Fine

Sunrise and sunset times for 11 Feb. 07.24, 17.05 G.M.T.; 12 May 04.13, 19.40 G.M.T.; 17 May 04.05, 19.48 G.M.T. These times are for Greenwich, Aberystwyth times being about 16 min. later.

be a characteristic of certain acid streams. The writer (1948) has recently studied a small mountain stream (the Amman) whose pH varies from 5·8 to 4·2. Frost (1939) found that the pH of the River Liffey at Ballysmuttan varies from 4·6 at flood to 6·8 after a prolonged drought, the normal being 5·6. Pierce (1947) notes that the Oklawaha River (Florida) has a pH range of 6·8–8·1, periods of acidity corresponding to periods of heavy rainfall when acid water is washed out of neighbouring swamps. The acidity of the Rheidol water is probably due to the presence of organic acids derived from the peaty soils of its upper reaches; there is no indication that carbon dioxide is responsible, for no diurnal pH swing has been detected, and the pH of water samples is not appreciably changed by boiling.

Butcher *et al.* (1937, p. 34) have studied the influence of peaty water on the composition of the water of the Tees, which rises in the moorland regions of Cross Fell. The Tees shows some variation of pH in relation to the rate of flow, but in this case the correlation is not as clear as in that of the Rheidol. This is not surprising, however, for near its source the Tees flows over limestone from which its water derives a variable amount of temporary hardness.

The temperature records for 14 January to 5 March, set out in Fig. 5 and Table 1, show that during the winter the water temperature is generally 1–3° C. below the air temperature. A slow climb in the air readings (24 January to 31 January) is followed by a slow climb in the water readings; thus on 25 January the air temperature rose to 7·4° C., but the water temperature did not reach this level until 4 days later, and sudden elevations of the air temperature (29 February) may result in the river being 7° C. colder than the air so that a bottle filled with the river water will immediately stream with condensation. A sharp drop in the air reading, however, is speedily followed by the water, possibly because at such times the nights may be very cold, though on some days the lag may result in the river being warmer than the air (17–21 February). The frequent fluctuations in the level of the main-stream introduced a complicating factor during this series of observations, for it may be presumed that when the bulk of water carried by the river is increased it should respond more slowly to fluctuations in the air temperature.

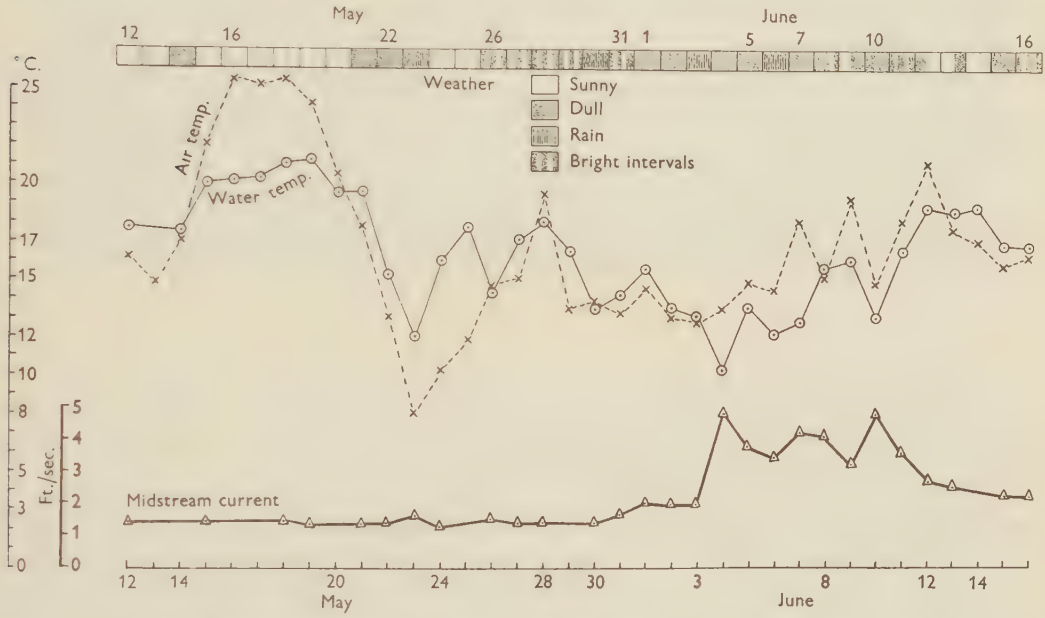


Fig. 7. Air temperature, water temperature, current speed and weather records for the Penybont area 12 May–16 June 1948. Water temperatures were taken at 15–16 hr. G.M.T. Air temperatures are shade maxima for each day. The weather index is explained at the head of Table 3.

A further series of temperature observations was begun on 12 May and continued until 16 June; these are given in Fig. 7 and Table 3. Over the greater part of this period the river remained at low level, and each day the general state of the weather was recorded. For this series the water temperatures were taken at 15.00–16.00 hr. G.M.T. for observations on the diurnal temperature variation (recorded in Fig. 6 and Table 2) showed that the daily maximum is attained at about

this time. The air temperatures are shade maxima for each day.

Table 3. *Current speed, air temperature, water temperature and weather data for the River Rheidol at Penybont, 12 May to 16 June 1948*

In the last column the general state of the weather for the day is recorded. 'Sunny' implies a day of uninterrupted sunshine or one in which the sun was obscured for very brief periods; 'dull' a dry day with brief intervals of sunshine or none at all; 'rain' a day of uninterrupted rain or frequent and prolonged showers; 'bright intervals' implies a day with sunny and cloudy periods, perhaps with light showers. Where any significant change took place in the weather on any particular day this is recorded (as for instance on 31 May).

Date	Air temp. (° C.)	Water temp. (° C.)	Current (ft./sec.)	Weather
12 May	16·2	17·7	1·4	Sunny
13	14·8	—	—	„
14	17·0	17·6	—	Dull
15	22·0	20·0	1·4	Sunny
16	25·5	20·1	—	„
17	25·2	20·2	—	„
18	25·4	21·0	1·4	„
19	24·2	21·2	1·35	„
20	20·5	19·5	—	„
21	17·7	19·6	1·35	Dull
22	13·0	15·2	1·35	Dull
23	8·0	12·0	1·6	Rain
24	10·2	16·0	1·3	Sunny
25	11·8	17·7	—	„
26	14·7	14·3	1·5	Bright intervals
27	15·0	17·0	1·4	„
28	19·4	18·0	1·4	„
29	13·4	16·4	—	„
30	13·8	13·4	1·4	Rain
31	13·2	14·2	1·65	Bright intervals early, rain later
1 June	14·5	15·5	2·0	Dull
2	13·0	13·5	1·9	„
3	12·8	13·1	1·9	Rain
4	13·4	10·3	4·8	Dull
5	14·8	13·5	3·8	„
6	14·4	12·1	3·4	Rain
7	18·0	12·7	4·2	Dull
8	15·0	15·6	4·1	Bright intervals
9	19·3	16·0	3·2	Sunny early, dull later
10	14·7	13·0	4·8	Dull
11	18·0	16·5	3·5	Bright intervals
12	21·0	18·8	2·7	Dull early, sunny later
13	17·6	18·5	2·5	Sunny early, dull later
14	17·0	18·8	—	Sunny
15	15·7	16·7	2·2	Dull
16	16·1	16·7	2·2	Bright intervals

When these air and water temperature readings are considered, in relation to the weather records, it will be noticed that during the warm and sunny period at the beginning of the series the water temperature did not rise above 21·2° C. even after 4 days of warm sunshine. This period was followed by a cool spell and on 24 and 25 May, days with a low air temperature but very sunny, the water was nearly 6° C. warmer than the air. During the following week of cool and generally cloudy weather the air and water readings follow each other more closely. On 4 June, after heavy rain on the previous day, the level of the river suddenly rose, this was accompanied by a marked drop in the water temperature, and the flood period that followed was accompanied by a return to 'winter' conditions in that the water readings were generally below the air readings, on one occasion by over 5° C. (7 June).

In the flowing water of the main-stream (to which all the data apply) no vertical temperature stratification was detected. This is not surprising for Galtsoff (1924), in a study of the vertical distribution of temperature in the Mississippi, states that for the river as a whole the difference between bottom and surface temperatures is usually less than 1° C. Carpenter (1928, p. 119) gives some temperature records for the Rheidol; 19·5° C. appears to be the maximum observed (9 August 1926). Berg (1943, p. 117) gives rather higher values for the Susaa—up to 24·8° C. in June 1940, and American rivers appear to be considerably warmer; thus Eddy (1932) found that the water temperature of the Sangamon river in Illinois ranged from 25 to 28° C. in July, and Murray (1938, p. 96) found many streams in northern Indiana whose maximum temperature exceeded 83° F. (28° C.).

On the whole it would appear that temperature conditions in the Rheidol are favourable for the development of a rich fauna. The river rarely freezes and the maximum temperatures so far observed are well within the thermal limit of brown trout (according to Murray, 1938, about 29° C.), and apparently within the range of stenothermous species like *Planaria alpina*, which is fairly common. Furthermore, it has been noted that during sunny weather in spring the water temperature may be raised several degrees above the air temperature, and it is possible that in this way the rapid development of plant and animal life at this time of the year may be encouraged. Temperature appears to be a very important factor determining the speed of growth of aquatic insects; thus Ide (1935) has shown that the richness of the Ephemerid fauna of streams is largely determined by the water temperature; Murphy (1922) showed that *Baetis* may complete its life cycle in 6 months, whereas a winter life cycle occupies 9 months. The observations of Rawlinson (1939) are particularly interesting; working on the life history of *Ecdyonurus venosus*

Photo 4. The falls above collecting station D.

Photo 5. The river at Penybont; the photograph is taken from the bridge, looking east. This is the section of the river to which the current speed, pH, oxygen and temperature records apply.

(Fab.) in the River Alyn, Denbighshire, North Wales, she found that summer broods of nymphs could complete their development in 1–2 months, but nymphs hatched in October took 7 months to reach their final instar. Rawlinson's temperature records (1939, p. 445) show that the rapid summer development corresponds to a water temperature of about 60° F. (15·5° C.).

Oxygen concentrations were measured by the standard Winkler method using 200 ml. samples taken as described above and N/80 thiosulphate solution. As a check on the accuracy of the method periodical determinations were made of the oxygen content of distilled water saturated with air, as recommended by Krogh (1916, p. 48); this has the advantage of checking the whole technique. The first determinations of the oxygen content of the main-stream water made in January all showed some degree of undersaturation; later, as the days grew longer, higher values were recorded and the first supersaturation sample was taken on 8 February (101 %). Subsequently the oxygen determinations varied between 98·2 and 101·8 % until 3 March. The observations on the variation in the oxygen content during the course of 1 day, made on 11 February (Fig. 6), show that the maximum concentration (in percentage of saturation) is only maintained for a relatively brief period in the middle of the day, and further observations on 12 and 17 May (Fig. 6) indicate that the same conditions seem to prevail during sunny, spring weather. Thus it will be noted that on 17 May, a clear day of uninterrupted sunshine and about 16 hr. of daylight, the oxygen concentration exceeded saturation for less than 6 hr. Facilities did not permit of any study of the oxygen content swing during the hours of darkness, and the observations set out in Fig. 6 were mainly designed to check the best time of day for taking day to day records.

The highest oxygen concentration (in percentage of saturation) observed in the main-stream is only 101·8; this was on 29 February 1948, a sunny day when the river bed was green with spring algal growth (*Stigeoclonium*). Much higher degrees of supersaturation are recorded for some other rivers. Butcher, Pentelow & Woodley (1930) have shown that turbulent streams readily give up an excess of oxygen to the air, whereas sluggish streams are more prone to accumulate an excess when there is active photosynthesis by their flora; thus in the River Itchen, described as a clear, rapid, unpolluted stream, oxygen values ranged from 68 to 125 %, while the River Lark, described as a slow stream, with very abundant diatoms and larger plants, proved to have a much more variable oxygen content ranging from 2 to 178 %.

In the Tees (Butcher *et al.* 1937, p. 39) it would appear that the oxygen content is mainly dependent on the degree of development of the algal flora. At times a luxuriant growth of *Cladophora* appears and the oxygen content then performs a 60–160 % diurnal swing; when this abnormal growth of alga is not present the diurnal variation is much less; thus the graph for 7–8 August 1929 (Butcher *et al.* 1937, p. 39) appears to show a range of about 85–90 %. The normal degree of oxygenation of very large rivers may be somewhat lower; thus Wiebe (1927, p. 143) gives data for the oxygen content of the unpolluted upper reaches of the Mississippi at Camden; the average for September 1926 was 80·0 %, for August 74·0 %. Berg (1943, p. 130) has published an extensive series of oxygen data for the Susaa ranging from 1 % (25 July 1939) to 100 % (18 March and 20 April 1939). These are for midstream; much higher values, up to 218 %, were noted for samples taken in vegetation near the bank. Unfortunately, the time of day when the samples were taken is seldom indicated.

It is probable that in rivers supersaturation with oxygen can only result from photosynthesis; how far the oxygen content can be brought up to saturation by the agitation of the water and direct pick-up from the air does not appear to be known with certainty and the problem requires further study. It is probable that direct absorption of gases from the air is of considerable importance even in somewhat sluggish streams, for Thompson (1925) has recorded that when the Illinois river becomes frozen over the oxygen content of the water may be so seriously reduced as to result in the death of fish. It is interesting to find that when the days are very short the oxygen content of a very fast, clear, shallow and unpolluted stream (the Rheidol) is always somewhat below saturation; at this time of the year the comparatively low temperature greatly increases the absolute amount of oxygen the water may contain, but it is evident that the frequently made assumption that turbulent streams are always 'fully' oxygenated (see, for instance, Embody, 1928, p. 21) is not warranted. Welch (1935, p. 371) has drawn attention to the inaccuracy of the time-worn statement that the lotic fauna is composed typically of animals whose dissolved oxygen demand is such that it can be fulfilled only by the highly oxygenated water of streams.

(*d*) *Chemical*

Some results of analyses of the river water are set out in Table 4. The samples were all taken from the main-stream; the methods employed follow closely those used by Pyefinch (1937), and have been described in my paper on the fauna of streams in the Black Mountain district of South Wales (1948). These analyses are not complete, but they are sufficient to show that the water of the river is very soft and that its composition varies little with changes in the level of the main-stream. Data for two other streams are included in Table 4; the great similarity between the

water of the Rheidol and that of the Amman will be noted, the latter being a very acid mountain stream which has its source in peaty soil. White River, Indiana, is an example of a river with hard water.

It has not been considered necessary to make any tests for the presence of lead. Since the earlier survey of Laurie & Jones (1938), which dealt with the condition of the river in 1931–2, there has been no renewal of pollution and 11 years ago James (1937) reported that there was, at that time, no detectable metallic pollution of the river in any part of its course. Sticklebacks are always to be found in its lower reaches, migratory fish penetrate as far as the falls at station D, the river has been stocked with trout and the fishing is protected. There is every indication that fish are more sensitive to the toxic action of dissolved lead salts than any other type of aquatic animal, and their uninterrupted occurrence in the river may be taken as satisfactory evidence that no significant amount of lead is present in the water.

Table 4. *Chemical data*

Alkali reserve is given in normality and pH in the usual units. All other figures are mg./l. tr., trace; nm, not measurable; a dash implies no determination.

Station	Date	Level	pH	Ca	Mg	Fe	Cl	SO_4	Alk. res.
			River Rheidol						
B	29 Nov. 1947	Normal	6·0	2·6	—	nm	10·2	—	0·00006
E	23 Nov. 1947	Heavy flood	5·8	2·0	1·2	—	8·4	—	0·000012
E	26 Nov. 1947	Flood subsiding	6·0	2·0	1·5	—	10·1	—	0·00004
E	28 Nov. 1947	Slightly above normal	6·2	3·2	2·0	—	10·0	8·4	—
E	4 Dec. 1947	Normal	6·3	3·4	1·5	nm	10·1	—	0·000065
E	21 Feb. 1948	Normal	6·3	3·2	—	nm	9·9	8·1	0·00012
			River Amman (Jones, 1948)						
		Normal	5·2	2·8	1·2	tr.	8·8	9·0	nm
			White River, Indiana (Denham, 1938)						
			7·8	74·0	29·0	0·15	78·0*	58·0	—

* Probably due to sewage.

3. THE FLORA

As this study is primarily zoological no intensive investigation of the flora has been carried out, but it presents some general features of interest in relation to the animal population. Phanerogamic vegetation is practically confined to the lower reaches of the river, and even here the main-stream is almost completely devoid of flowering plants except in places where high banks confine the river to a constant course and deposits of sand and silt form a suitable substratum as, for instance, in the Penybont area. Here many clumps of *Ranunculus aquatilis* and *Callitriche aquatica* grow in the flowing water, and the margins of the river are bordered with *Glyceria fluitans*. These plants grow abundantly in the backwaters, together with occasional patches of *Potamogeton* and *Lemna*.

At station A *Fontinalis antipyretica* grows abundantly on the large, rough stones, and there is a widespread but ragged growth of the moss on the rocky bed at station B. *Fontinalis* also grows in some of the rock pools at station C, together with the liverwort *Aplozia crenulata*. At stations D and E occasional clumps of *Fontinalis* occur at the margins of the river, in rock pools, and in a few places where there are large stones firmly fixed in the river bed; the shallow riffles are generally quite devoid of bryophytes.

In her study of the microflora of the Rheidol, Reese (1937) has recorded nearly 60 species of algae. The most abundant, according to her list (1937, p. 405), were *Chamaesiphon incrustans*, *Chamaesiphonopsis regularis*, *Phormidium tenue*, *Stigeoclonium falklandicum*, *Achnanthes* spp., *Tabellaria flocculosa*, *Gomphonema* spp., *Batrachospermum moniliforme* and *Lemanea mammillosa*. *Ulothrix* and *Mougeotia* were also present, but not abundant. Reese's observations apply mainly to the Ponterwyd and Cwm Rheidol sections of the river (stations B and D).

A luxuriant growth of *Stigeoclonium* appeared at most parts of the river in March and April 1948; in the Whitebridge area bright yellow-green tufts covered the stones and some *Draparnaldia glomerata* was also seen. *Stigeoclonium* was also the dominant alga of the backwaters, together with quantities of *Tabellaria* and some *Rhizoclonium hieroglyphicum*. By the third week of May the *Stigeoclonium* had practically disappeared at stations B–E, the river bed reverting to grey-brown. *Tabellaria*, *Fragilaria* and *Synedra* then appeared to be the chief algae in the backwaters, and

scrapings from stones on the riffles contained many *Cosmarium* and *Closterium*. In June algal growth appeared very scanty in the lower reaches of the river, but when station A was visited, towards the end of the month, the stream-bed was found covered with an abundant green-brown growth mainly composed of *Stigeoclonium*, *Mougeotia*, *Tabellaria* and *Batrachospermum*.

Lemanea mammillosa is very widely distributed in the main-stream, particularly on the rocky bed of region B. In spring very numerous small tufts of this alga occur on stones on many of the riffles, and an abundant growth is developed on large boulders carrying the full force of the current.

4. THE FAUNA

(*a*) *The species recorded*

The study of the fauna was carried out in the same general way as that adopted in my previous studies. A total of 26 faunal samples was taken, on the dates set out at the head of Table 5. Each sample at B, C and D involved approximately 1 hr. collecting; each at

Table 5. *The fauna*

R, rare; F, few; C, common; N, numerous; VN, very numerous. For explanation see below, p. 84.

Habitats are given in the last column according to the following index. Where more than one figure is given the *first* indicates the favourite habitat and the others refer to situations where the species is less commonly found. It will be understood that this index applies strictly to the Rheidol.

1 Large stones in swift water and moss upon them.
2 Stones and pebbles in moderately swift water.
3 Pebbles and gravel, sand or silt in slowly flowing water.
4 Stones in rock pools in the main-stream.
5 Gently flowing open water.
6 *Glyceria* and other vegetation at the margins of flowing water.
7 Phanerogamic vegetation in the main-stream.
8 Sand-mud-debris bottom of quiet pools of the main-stream.
9 Vegetation of backwaters.
10 Sand-mud-debris bottom of backwaters.
11 Surface or open water of backwaters.
12 Silt and stones in small, shallow backwaters with no macroflora.
13 In moss and other vegetation in rock pools separated from the main-stream at normal level, or on their surface.
14 In clear, silt-bottomed rock pools separated from the main-stream at normal level.
15 Large isolated stones on bottom of muddy backwaters.
16 Under stones on the edge of flood beaches.

Collecting station	A	B	C	D	E	
Collecting dates (Oct. 1947–June 1948) ...	27 Apr.	18 Oct.	1 Nov.	19 Oct.	15–17 Oct.	
	23 June	29 Oct.	7 Dec.	19 Dec.	18 Nov.	
		23 Jan.	6 Mar.	31 Dec.	29 Feb.	
		10 Mar.	21 Apr.	28 Feb.	11–14 Mar.	
		22 Apr.	20 June	18 Apr.	20–23 Apr.	
		22 May		29 May	1–8 May	
					22–24 June	Habitat
HYDROZOA						
Hydra viridissima Pall.	—	—	—	—	R	9
PLATYHELMIA						
Polycelis nigra Müll.	—	—	—	—	F	6
Planaria vitta Dugés	C	R	R	R	R	2
P. alpina (Dana)	—	—	—	F	C	1, 2
OLIGOCHAETA						
Lumbriculus variegatus (Müll.)	C	N	R	R	N	8, 10, 3, 14
Eiseniella sp.	—	—	—	—	R	8
Chaetogaster sp.	—	—	—	—	C	8
Nais sp.	R	—	—	—	C	10, 3
MOLLUSCA						
Ancylastrum fluviatile (Müll.)	—	R	F	N	C	2, 4
Limnaea pereger (Müll.)	—	—	—	—	C	9
Pisidium sp.	—	—	—	—	R	8
HIRUDINEA						
Herpobdella octoculata (L.)	F	—	—	—	C	15, 3
Glossosiphonia complanata (L.)	—	—	—	—	F	15

Table 5 (*continued*)

Collecting station	A	B	C	D	E	
Collecting dates (Oct.1947–June 1948) ...	27 Apr. 23 June	18 Oct. 29 Oct. 23 Jan. 10 Mar. 22 Apr. 22 May	1 Nov. 7 Dec. 6 Mar. 21 Apr. 20 June	19 Oct. 19 Dec. 31 Dec. 28 Feb. 18 Apr. 29 May	15–17 Oct. 18 Nov. 29 Feb. 11–14 Mar. 20–23 Apr. 1–8 May 22–24 June	Habitat
CRUSTACEA						
Ilyocryptus sordidus (Liev.)	—	—	—	—	N	8, 10
Eurycercus lamellatus (Müll.)	—	N	—	—	—	8
Alonopsis elongata Sars	—	—	—	—	F	9
Alona affinis (Leydig)	—	—	—	—	F	9
Chydorus sphaericus (Müll.)	—	—	—	—	C	9
Cypria exsculpta (Fischer)	—	—	—	—	R	8
Candona sp.	—	—	—	—	R	8
Canthocamptus staphylinus (Jurine)	—	—	—	—	F	9
Cyclops fuscus Jurine	—	—	C	C	F	12, 13, 9, 3
C. albidus Jurine	—	C	F	—	N	9, 8, 13
C. agilis Koch, Sars		—	—	—	N	7, 10
C. viridis (Jurine)	—	C	F	—	—	8, 13
C. macruroides Lillj.	—	—	—	—	F	9
HYDRACARINA						
Diplodontus despiciens (Müll.)	—	—	—	R	—	3
Sperchon undulosus Koen.	R	—	—	—	R	3
Pseudosperchon verrucosus (Protz.)	R	—	—	R	—	2
Limnesia koenikei Piers.	—	—	—	—	C	6, 9
Lebertia sp.	C	R	R	R	N	8, 10, 2, 9
Gnaphiscus setosus Koen.	—	—	—	—	C	9
Hygrobates longipalpis (Herm.)	—	R	R	R	VN	9, 3, 7, 10
H. naicus (Johnst.)	F	—	—	—	—	2
Megapus nodipalpis Sig Thor	—	—	—	—	R	1
Wettina podagrica (C. L. Koch)	—	—	—	—	N	9, 6, 3
Forelia liliacea (Müll.)	—	—	—	—	C	9
Aturus scaber Kram.	—	—	—	—	R	3
Brachypoda versicolor (Müll.)	—	—	—	—	N	9
Mideopsis orbicularus (Müll.)	—	—	—	—	R	9
Arrhenurus robustus Koen.	—	—	R	—	—	13
A. cylindratus Piers.	—	—	—	—	R	9
Arrhenurus sp. *a*	—	—	R	—	—	13
Piona coccinea (C. L. Koch)	—	—	—	—	R	7
COLLEMBOLA						
Isotomurus palustris (Müll.)	—	—	—	—	R	5
PLECOPTERA						
Perlodes mortoni (Klap.) (bred out)	R	N	F	C	C	1, 2, 13
[1]Isogenus nubecula Newm.?	—	R	R	R	—	4, 3
Isoperla grammatica (Poda) (bred out)	R	N	R	C	C	2
[2]Chloroperla torrentium (Pict.) (bred out)	N	VN	R	VN	VN	2, 1, 3
C. tripunctata (Scop.) (bred out)						
Brachyptera risi (Mort.)	—	—	—	F	C	2, 6
Leuctra fusciventris Steph. (bred out)	C	VN	F	N	N	2, 1
L. inermis Kemp. (bred out)						
L. hippopus Kemp. (bred out)						
L. nigra (Oliv.) (bred out)						

[1] This is a large stonefly similar in size to *Perlodes mortoni*, but the head is dark in front of the M-line, the last joint of the maxillary palp is sharply pointed, the pronotum is more rectangular, and there is a brush of setae on the inside of the lacinia. I have not succeeded in breeding out any adults.

[2] A number of adults of both species of *Chloroperla* were reared from nymphs taken in the river, but as the nymphs cannot be distinguished the distribution and relative abundance of the two species cannot be given with any degree of certainty. The same applies to *Leuctra* and *Baetis*.

Table 5 (*continued*)

Collecting station	A	B	C	D	E	
Collecting dates (Oct. 1947–June 1948) ...	27 Apr. 23 June	18 Oct. 29 Oct. 23 Jan. 10 Mar. 22 Apr. 22 May	1 Nov. 7 Dec. 6 Mar. 21 Apr. 20 June	19 Oct. 19 Dec. 31 Dec. 28 Feb. 18 Apr. 29 May	15–17 Oct. 18 Nov. 29 Feb. 11–14 Mar. 20–23 Apr. 1–8 May 22–24 June	Habitat
PLECOPTERA (*continued*)						
Protonemura meyeri (Pict.) (bred out)	R	F	R	C	N	2, 3, 8
Amphinemura cinerea (Oliv.) (bred out)	R	N	R	C	C	2, 3, 6
Nemoura variegata Oliv.	—	—	R	R	—	2
EPHEMEROPTERA						
Leptophlebia sp.	—	—	—	—	R	9
Paraleptophlebia sp.	—	R	—	—	R	2
Ephemerella sp.	C	—	R	C	N	3
Caenis sp.	—	—	—	—	F	15
Baetis scambus Eaton (bred out) B. rhodani (Pict.) (bred out) B. pumilus (Burm.) (bred out)	N	VN	R	VN	VN	2, 1, 9, 6, 7
Siphlonurus lacustris Eaton (bred out)	N	—	N	—	VN	7, 10, 12, 9, 14
Heptagenia lateralis (Curt.) (bred out)	—	—	—	—	VN	2
Ecdyonurus venosus (Fabr.)	—	R	—	F	—	2
Rhithrogena semicolorata (Curt.) (bred out)	—	C	—	VN	VN	2
ODONATA						
Cordulegaster boltonii (Donov.)	—	—	R	—	F	7, 8, 14
Libellula quadrimaculata L.	—	R	—	—	—	8
Pyrrhosoma nymphula (Sulz.)	—	—	C	—	C	9, 13, 7
Ischnura elegans (van der Linden)	—	—	—	—	C	9
Coenagrion puellum (L.)	—	—	—	—	F	9
HEMIPTERA						
Hydrometra stagnorum (L.)	—	—	—	R	C	11, 5, 16
Velia currens (Fab.)	—	N	F	C	C	5, 6, 13
Gerris najas (Degeer)	—	C	F	N	C	5, 14
G. thoracicus Schum.	—	—	—	—	R	11
G. gibbifer Schum.	—	—	N	—	R	13, 14
G. lacustris (L.)	—	—	F	R	N	11, 5, 14
Nepa cinerea L.	—	—	—	—	R	10
Notonecta maculata Fab.	—	—	C	—	—	13
N. glauca L.	—	—	—	—	F	9, 11
N. obliqua Gall.	—	—	—	—	R	9, 11
Corixa punctata (Illig.)	—	—	—	—	R	9
C. linnei (Fieb.)	—	—	—	—	R	9
C. sahlbergi (Fieb.)	—	—	R	—	C	9, 14
C. castanea (Thoms.)	—	—	—	—	R	9
C. striata (L.)	—	—	—	—	VN	9
C. distincta (Fieb.)	—	—	—	—	R	9
C. semistriata (Fieb.)	—	—	—	—	N	9
Micronecta sp.	—	—	—	—	F	6
Corixidae spp. nymphs	—	—	—	VN	VN	8, 9, 10
MEGALOPTERA						
Sialis lutaria (L.)	—	R	—	—	C	8
TRICHOPTERA						
Limnophilus marmoratus Curt.	—	—	—	—	R	9
Anabolia nervosa (Curt.)	—	—	—	—	VN	10, 8, 9, 6, 3
Stenophylax stellatus (Curt.)	R	R	R	—	C	3
Halesus radiatus (Curt.)	C	F	F	—	F	3, 6, 13, 7
H. auricollis (Pict.)	R	C	N	—	—	13, 4, 3
Drusus annulatus (Steph.)	R	R	—	—	—	2
Sericostoma personatum (Spence)	—	R	—	C	C	3, 8
Goëra pilosa (Fab.)	—	—	—	—	R	2

Table 5 (*continued*)

Collecting station	A	B	C	D	E	
Collecting dates (Oct. 1947–June 1948) ...	27 Apr.	18 Oct.	1 Nov.	19 Oct.	15–17 Oct.	
	23 June	29 Oct.	7 Dec.	19 Dec.	18 Nov.	
		23 Jan.	6 Mar.	31 Dec.	29 Feb.	
		10 Mar.	21 Apr.	28 Feb.	11–14 Mar.	
		22 Apr.	20 June	18 Apr.	20–23 Apr.	
		22 May		29 May	1–8 May	
					22–24 June	Habitat
TRICHOPTERA (*continued*)						
Silo pallipes (Fab.)	—	—	—	R	—	2
Lepidostoma sp.	—	R	—	—	F	2
Bereodes minuta (L.)	—	—	—	—	R	10
Odontocerum albicorne (Scop.)	—	—	—	—	R	3
Leptocerus aterrimus Steph.	—	—	—	—	N	15, 9
Mystacides azurea (L.)	—	—	—	—	VN	9, 8, 6
Hydropsyche instabilis (Curt.)	C	C	R	C	C	1, 4
Plectrocnemia conspersa (Curt.)	C	R	R	R	R	2, 3, 4
Polycentropus flavomaculatus (Pict.)	C	N	R	C	F	2, 3
Rhyacophila dorsalis (Curt.)	R	F	R	C	N	1
[1]Rhyacophila sp. *a*	—	—	—	R	F	1
Glossosoma boltoni Curt.	—	—	—	F	VN	1, 2, 3
Oxyethira sp.	—	R	R	R	C	8, 4, 9, 13
COLEOPTERA (imagines)						
Haliplus ruficollis (Degeer)	—	—	—	—	R	6
H. lineatocollis (Marsh.)	—	—	—	—	C	6, 7, 9
Laccophilus hyalinus (Degeer)	—	—	—	—	R	9
Bidessus minutissimus (Germ.)	—	—	—	—	C	3, 12, 10
Deronectes latus (Steph.)	—	—	—	—	R	6
D. elegans (Panz.)	—	—	—	—	C	6, 7
D. duodecimpustulatus (Fab.)	—	—	—	—	R	3
Oreodytes rivalis (Gyll.)	F	F	—	F	F	2, 6
O. septentrionalis (Gyll.)	R	R	—	F	F	2, 3, 6
O. davisii (Curt.)	—	R	F	R	F	2, 6, 14, 12
Hydroporus pictus (Fab.)	—	—	—	—	C	9
H. lepidus (Oliv.)	—	—	N	—	R	14, 13, 6
H. palustris (L.)	—	—	—	—	C	9
H. tristis (Payk.)	—	—	—	—	R	9
H. erythrocephalus (L.)	—	—	—	R	—	13
H. pubescens (Gyll.)	—	—	—	—	R	9
Colymbetes fuscus (L.)	—	—	—	—	R	9
Agabus guttatus (Payk.)	—	—	R	—	—	14
A. didymus (Oliv.)	—	—	R	—	F	9, 13
A. paludosus (Fab.)	—	—	F	—	F	13, 9
A. sturmii (Gyll.)	—	—	—	—	R	9
A. bipustulatus (L.)	—	—	C	—	R	13, 9
Platambus maculatus (L.)	R	—	—	–	R	9, 3
Illybius fuliginosus (Fab.)	—	—	—	—	R	9
Dytiscus marginalis L.	—	—	—	—	R	6
D. semisulcatus Müll.	—	—	—	—	R	6
Gyrinus natator v. substriatus Steph.	—	—	R	—	C	6, 11, 13
[2]Orectochilus villosus (Müll.)	—	—	—	—	C	16, 3
Hydrobius fuscipes (L.)	—	—	—	—	R	9
Anacaena globulus (Payk.)	—	R	—	—	—	6
Laccobius minutus (L.)	—	—	—	—	N	9
Limnebius truncatellus (Thunb.)	—	—	R	R	—	13
Helophorus aquaticus (L.)	—	—	—	—	R	9
H. brevipalpis Bedel	—	—	—	—	R	9

[1] With gills in bunches of four as in the continental species *Rhyacophila glareosa* McLachl.

[2] *Orectochilus* is nocturnal (Fowler, 1887, p. 217) and seems to hide during the day beneath stones at the edge of the stream.

Table 5 (*continued*)

Collecting station	A	B	C	D	E	
Collecting dates (Oct. 1947–June 1948) ...	27 Apr. 23 June	18 Oct. 29 Oct. 23 Jan. 10 Mar. 22 Apr. 22 May	1 Nov. 7 Dec. 6 Mar. 21 Apr. 20 June	19 Oct. 19 Dec. 31 Dec. 28 Feb. 18 Apr. 29 May	15–17 Oct. 18 Nov. 29 Feb. 11–14 Mar. 20–23 Apr. 1–8 May 22–24 June	Habitat
Coleoptera (imagines) (*continued*)						
Hydraena gracilis Germ.	R	—	—	—	R	3
Elmis aenea (Müll.)	C	R	R	R	R	2, 3, 13, 8
Latelmis volkmari (Pz.)	F	C	R	F	C	2, 3, 13, 8
Esolus parallelopipedus (Müll.)	R	—	—	R	C	2, 3
Limnius tuberculatus Müll.	N	C	R	R	C	1, 2, 3, 13
Dryops luridus Er.	R	—	—	R	—	3
Coleoptera (larvae)						
Dytiscus spp.	—	—	—	—	R	6
Other Dytiscidae	—	F	C	R	C	9, 8, 6, 13
Gyrinidae	—	R	—	C	C	2
Haliplidae	—	—	—	—	R	10
Helodidae	—	—	—	N	—	3, 4
Dryops sp.	F	F	—	F	C	2, 3
Elminae	C	R	—	R	C	1, 2
Diptera (larvae)						
Pedicia sp.	R	R	R	R	R	12, 13
Limnophila sp.	R	R	—	R	—	3, 12
Dicranota sp.	R	C	—	R	—	3, 12, 8
Tipula spp.	R	F	—	F	C	8, 12, 3
Pericoma sp.	—	—	—	—	R	9
Dixa sp.	—	—	R	—	R	13, 9
Simulium angustitarse Lundst.	—	—	—	R	R	1
S. ornatum Meig.	R	R	—	—	N	1
S. tuberosum Lundst.	R	—	—	N	—	1, 2
S. reptans (L.)	—	VN	—	VN	VN	1
S. latipes (Meig.)	—	R	—	—	—	1
Tabanus sp.	—	—	—	R	R	3, 8, 12
Limnophora sp.	—	—	—	—	R	9
Sepedon sp.	—	—	—	—	R	9
Atherix sp.	—	—	—	C	R	3, 12
Pentaneura sp. *a*	R	R	R	C	F	3, 8, 12, 10
Pentaneura sp. *b*	—	—	—	—	R	10
Anatopynia sp.	—	N	—	—	R	8, 3
Corynoneura sp.	—	—	—	R	N	9, 3
Metriocnemus sp.	—	—	—	R	F	8
Prodiamesa olivacea (Meig.)	—	R	—	—	C	8
Cricotopus sp.	—	C	—	—	R	2, 4
Hydrobaenus sp.	R	—	—	—	N	1, 2
Ceratopogonidae (Bezzia type)	—	—	—	—	F	10, 8
Chironomus						
s.g. Stictochironomus	—	—	—	—	N	8
s.g. Microtendipes	—	R	—	R	VN	8
s.g. Endochironomus	—	VN	—	—	F	8
s.g. Chironomus	—	—	—	—	C	8
Tanytarsus sp. *a*	—	N	N	—	N	8, 13, 14
Tanytarsus sp. *b*	—	—	—	—	C	8
Diptera (pupae)						
Simulium reptans (L.)	—	VN	—	VN	VN	1
S. monticola Fried.	—	—	—	F	—	1
Chironomus (Microtendipes) pedellus (Degeer)	—	—	—	—	C	8

Table 5 (*continued*)

Collecting station	A	B	C	D	E	
Collecting dates (Oct. 1947–June 1948) ...	27 Apr.	18 Oct.	1 Nov.	19 Oct.	15–17 Oct.	
	23 June	29 Oct.	7 Dec.	19 Dec.	18 Nov.	
		23 Jan.	6 Mar.	31 Dec.	29 Feb.	
		10 Mar.	21 Apr.	28 Feb.	11–14 Mar.	
		22 Apr.	20 June	18 Apr.	20–23 Apr.	
		22 May		29 May	1–8 May	
					22–24 June	Habitat
DIPTERA (pupae) (*continued*)						
Chironomus						
s.g. Endochironomus	—	—	—	—	F	8
s.g. Stictochironomus	—	—	—	—	F	8
Tanytarsus spp.	—	—	—	—	C	8
VERTEBRATA						
Gasterosteus aculeatus L. (3-spined stickleback)	—	—	—	—	N	6, 7, 9
Salmo trutta L. (brown trout)	C	C	C	C	C	
Anguilla anguilla (L.) (eel)	—	—	—	R	R	
Rana temporaria L. (spawn and tadpoles)	—	—	C	—	C	13, 9
Triturus vulgaris L. (newt)	—	—	R	R	—	13

Table 6. *Analysis of Table* 5

Animal group	Total number of species	Main-stream species (habitats 1–8)
HYDROZOA	1	—
PLATYHELMIA	3	3
OLIGOCHAETA	4	4
MOLLUSCA	3	2
HIRUDINEA	2	1
CRUSTACEA	13	8
HYDRACARINA	18	11
COLLEMBOLA	1	1
PLECOPTERA	13	13
EPHEMEROPTERA	11	9
ODONATA	5	3
HEMIPTERA	18	5
MEGALOPTERA	1	1
TRICHOPTERA	21	18
COLEOPTERA	41	23
DIPTERA	31	24
VERTEBRATA	5	4
Total	191	130
Insecta	142	97

station E included a complete investigation of the Whitebridge and Penybont areas, a collecting time of about 2 hr., and was sometimes spread over a period of days, as the dates indicate. Station A could only be visited twice; on each occasion about an hour and a half was spent in collecting and the ease and completeness with which the river can be examined at this station compensates, in some degree, for the small number of samples taken. The methods used have been described fully in previous studies, see Jones (1941, pp. 16–17) and Jones (1948, p. 56).

The habitat of most of the larger species could be noted in the field. To check the distribution of smaller species samples from different habitats (e.g. vegetation in backwaters; sieved sand and debris from the bottom of a main-stream pool) were kept separate until examined in the laboratory. The works consulted for identification include those listed by Laurie (1942) and others cited in my paper on the Black Mountain streams (1948). In the case of the insects the nomenclature of genera, subgenera and species follows the Check List of Kloet & Hincks (1945).

All the animals are listed in Table 5, which gives their distribution, habitats and degree of abundance. This list does not include any records previous to October 1947. No quantitative sampling was attempted and the records for the degree of abundance are based on general observation in the field and the numbers of individuals found in the fauna samples. R (rare) denotes species rarely taken, of which the total number of individuals captured at the collecting station was not more than 5. F (few) refers to species somewhat more frequently encountered; total number 5–20. Animals moderately common, but never abundant, of which the total number captured at the collecting station was up to 100 are denoted as common (C). N (numerous) denotes more abundant species totalling 100–200 individuals, and VN (very numerous) those of which the number captured could be estimated at several hundreds.

(*b*) *Remarks on the fauna*

The analysis of the faunistic data in Table 6 shows that the animal population includes 191 species; this figure is a minimum, as some of the genera recorded may include more than one species. Of these 191 not

all have been found in the main-stream; species with habitats 1–8 number 130, and this figure includes a few whose primary habitat is in backwaters, e.g. *Herpobdella octoculata*, *Gerris lacustris* and *Anabolia nervosa*.

As might be expected the main-stream fauna is dominated by lotic types and of the main-stream species 97 are insects. Plecoptera are well represented at most parts of the river. *Perlodes mortoni*, *Chloroperla torrentium* and *C. tripunctata* were dominant types during the winter; *Perlodes* bred out in March and early April, and *Chloroperla* adults (both species) appeared from the first week in May to the first week in June. In the lower reaches of the river, at least, *tripunctata* is far more common than *torrentium*. Of the four species of *Leuctra*, *fusciventris* was found breeding out in October, *hippopus* bred out in February, *inermis* in April and *nigra* in May. Adults of *Isoperla grammatica* and *Amphinemura cinerea* began to appear in the second week in May. These records apply in the main to captures on the river bank, under stones on flood beaches, etc., but in the case of all the insects denoted as 'bred out' in Table 5 adults were reared in the laboratory from nymphs taken in the river.

The seasonal distribution of the common species of Ephemeroptera was as follows: *Baetis rhodani* was the dominant species in October, adults breeding out until late in November. In March very few nymphs were to be found, but large numbers of young ones appeared in April and more adults appeared in May and June. Some of these were of very large size compared with the autumn specimens. In December and during the winter *Rhithrogena* became the dominant type and bred out late in April; at this time great numbers of *Heptagenia* nymphs appeared in the lower reaches of the river, grew very rapidly and bred out in the third and fourth week of May. The chief summer form is *Siphlonurus lacustris* which breeds out in June and July. *Siphlonurus* does not like swiftly flowing water and is not found in the main-stream unless there is vegetation cover or some other shelter from the current.

The chief water-bug of the main-stream is *Gerris najas*. Adults appeared from their winter hiding-places in February and soon paired; young nymphs were seen in June. *G. gibbifer* is the typical species of the rock pools and *lacustris* the most abundant in backwaters. Cased types of Trichoptera are the most common in the lower reaches of the river; the little stony case of *Glossosoma* appears in great numbers on the riffles in early summer, and where there are pools with vegetable debris on the bottom *Mystacides azurea* larvae are to be found abundantly at most seasons of the year; swarms of the adults fly over the pools in June. *Anabolia nervosa* is abundant and widespread; the young larvae found in the winter months climb among plants, particularly *Glyceria* and *Callitriche*. Later they build much heavier cases and crawl on the bottoms of backwaters in numbers exceeding 100 per sq.ft. The backwater dwellers make cases mainly of vegetable material, but many large larvae found in the main-stream had very heavy, tapering cases made from small stones and gravel. Caseless Trichoptera are well represented too; in the lower reaches the dominant type is *Rhyacophila*; numbers of large larvae and pupae were found in early summer, the male pupae showed the genetalia pattern clearly and all appeared to be *R. dorsalis*. I have found no *R. obliterata* in the Rheidol (the species recorded by Carpenter, 1924, p. 14) though this is common in smaller streams in the Aberystwyth district.

Few of the many species of Coleoptera are numerous. *Hydroporus lepidus* is very common in the rock pools at station C, *Laccobius minutus* in vegetation in backwater G and *Limnius tuberculatus* in moss at station A. The dominant Dipteran, indeed the dominant animal of the river, is *Simulium reptans*. On the riffles in the lower reaches of the river this insect occurs in prodigious numbers; in April almost every stone in swift, broken water is covered with the larvae, and later in the month and early in May pupae appear in tightly packed groups of 50–100; six or more such groups may be found on one medium-sized stone. The young larvae of summer broods are found towards the end of June, and these occur not only on the riffles but on stones where the current is comparatively gentle.

Rawlinson (1939) has shown that *Ecdyonurus venosus* from the River Alyn, North Wales, appears to be a local variety of the species. It is possible that a number of local varieties like this occur in the Rheidol. Thus *Heptagenia lateralis* differs from the form as described by Kimmins (1942). The Rheidol *Perlodes mortoni* also appears to be a local variety. The details of these differences will be noted in another paper.

Though 130 species are recorded for the main-stream the fauna is not really rich. In early March it was possible to lift stone after stone from the stream-bed in the lower reaches of the river without revealing any type of animal life; at this time there was every indication that the animal population had suffered severely from the long-continued floods in January and February. It is probable that the violent flooding and the instability of the river bed are unfavourable factors; how far the acidity of the water is responsible for the lack of richness of the fauna is more doubtful. Frost (1939) has shown that in the acid upper reaches of the River Liffey brown trout are small and slow growing, whereas in the calcareous and alkaline lower course of the river trout grow rapidly and attain a much greater size. The examination of the stomach

contents of fish from both regions did not indicate that the smaller fish suffered from any scarcity of food, and a further study by Frost (1942) of the invertebrate fauna of mosses on the stream bed at Ballysmuttan where the pH range of the river is 4·4–6·8 and at Straffan, where it is 7·4–8·6, failed to reveal any significant difference in the total density of organisms present. In the Black Mountain district (Jones, 1948) the acid streams on the southern slopes of the mountain have a much poorer fauna than the alkaline stream on the north, but other factors, temperature, gradient and flood frequency are involved.

Whether lack of submerged vegetation substantially lessens the productivity of a stream-bed is also uncertain; Needham (1926, p. 196) found that all types of bottom except silt supported less than 2 g./sq.ft. of available fish food; his figures for rubble (i.e. large pebbles and loose rocks), coarse gravel, sand and bedrock are 1·88, 1·281, 0·46 and 0·0065 g./sq.ft. These figures apply to stream bottoms with 'little or no aquatic vegetation'. On the other hand, submerged plant beds of all types supported well over 2 g./sq.ft. The values for *Ranunculus aquatilis* and *Potamogeton americanus* are 3·51 and 5·85. Murray (1938) found that in Northern Indiana streams with a predominantly insect fauna, vegetated areas on the average have a higher population than non-vegetated areas. Murray's table (Table 4, p. 110) indicates a total organism frequency of 2338·8 for areas with vegetation and 1630 without. These are average numbers of animals per square metre. The same table gives a density of 2369 for 'gravel-sand', but whether this is with vegetation or without is not clear. Nevertheless, these differences are not very great and it would appear that in the lower Rheidol, where the river bed is composed of rubble, gravel and sand, a substantial increase in the amount of phanerogamic vegetation would be necessary to produce any really significant increase in the animal population.

In the Rheidol the general environmental conditions are not favourable for many species that normally inhabit streams and rivers in great abundance. The water is too acid for *Gammarus pulex*, which occurs in great numbers in alkaline streams; thus Whitehead (1935) records up to 214 per sample (4 sq.dm.) in the 'stony region' of a chalk stream in Yorkshire. Cladocera are not well represented even in the backwaters, probably because of the frequent floods; the only species I have found in the lower reaches of the main-stream is the curious creeping form *Ilyocryptus sordidus*, which lives in debris on the bottom of pools in the Penybont area. The swift current, the acidity of the water, the low calcium content, and the instability of the river bed are all adverse factors where Mollusca are concerned. The only species which inhabits the main-stream in any numbers is *Ancylastrum fluviatile*, and this is only found where the current is moderate and large stones, firmly lodged in the river bed, provide a stable substratum; none occurs on the shifting bottom of the riffles. *Limnaea pereger* does not occur in the main-stream at all, even where there beds of phanerogamic vegetation. In the River Towy, near Carmarthen, the snail occurs plentifully in the main-stream, in beds of *Myriophyllum*. At normal level the pH of the Towy is about 6·8.

Another absentee is the 'may-fly' *Ephemera danica*, whose absence may be due to its inability to withstand the swift current. Percival & Whitehead (1926, p. 143) have shown that *Ephemera* nymphs cannot swim faster than 2½ ft./sec. Corixidae are practically restricted to the backwaters, for there are very few pools in the main-stream affording them a suitable habitat. The fish fauna is decidedly poor, including only the three-spined stickleback, brown trout, sewin and eels. There are some uncertain records of salmon (*Salmo salar*). A conspicuous missing species is the minnow (*Phoxinus phoxinus*) which is abundant in the neighbouring rivers Teifi, Towy and Dovey. In the summer of 1941 the writer collected several hundred young minnows from the Dovey and placed them in backwaters in the Rheidol, but they do not appear to have survived. It is possible that the acidity of the water is too high for minnows; this is suggested by their distribution in the lakes in the Plynlimmon district; in Fron-goch lake, near Devil's Bridge, which has a pH of 6·8–7·0, there are immense numbers of them, but none seems to occur in similar lakes in the district which have more acid water (pH 6·0–6·4).

A detailed comparison of the present fauna of the Rheidol with that described in previous studies would occupy much space and presents certain difficulties. Carpenter (1924) did not suffix species authorities to her records so that it is not always possible to check the identity of her species with those recorded now. Now is it clear as to exactly where Carpenter examined the river or what collecting methods were used; according to her paper (1924, p. 13): 'The fauna is in all cases that of the main stream, and not that of either temporary or permanent "cut-offs", which may be understood to be influenced by conditions different from those affecting the river itself.' This statement does not definitely rule out backwaters. In the survey by Laurie & Jones (1938) main-stream and backwater species are not clearly distinguished, one of the collecting stations being well within the tidal area, the upper and middle reaches of the river were not studied, and certain animal groups, including the Oligochaeta, Crustacea, Hydracarina and Diptera were not examined in detail. Before our knowledge of the fauna of the river can be regarded as satisfactory the main-stream must be studied further, with some method of quantitative

sampling. This will have to be carried out on a considerable scale to yield results of value, for the fauna varies greatly in abundance from place to place and from season. A study of the food of Rheidol trout would also be of great interest, and the writer hopes that it will be possible to make arrangements for this to be done.

SUMMARY

1. This is an ecological study of a river which before 1922 suffered severely from lead pollution. After the cessation of mining activities in 1921 the fauna improved rapidly; for the last 10 years, at least, there has been no significant degree of pollution and the river may be regarded as having completely recovered.

2. The river draws nearly all its water from areas of high rainfall over 1000 ft. Its lowland course is short and its lowland tributaries few, so that the river retains its mountain character until it reaches the sea. In the upper and middle reaches the stream-bed is largely rocky, in the lower reaches it is composed of stones and gravel, with sand and silt where the current is slack, and very unstable.

3. The river is swift; just above the tidal area at Aberystwyth its flood velocity is nearly 6 ft./sec. and currents of over 3 ft./sec. are maintained for long periods in wet seasons. Currents on the riffles attain 4–5 ft./sec. even when the level of the main-stream is low.

4. The water is very soft (Ca 2·0–3·4 mg./l.) and acid, the pH varying from 6·4 at low level to 5·8 at full flood. During short winter days the oxygen content is high, but always somewhat below saturation, and on sunny days in spring only slight degrees of supersaturation are observed (up to 101·8%).

5. During winter the day temperature of the water is usually 1–3° C. below the air temperature. In cool, sunny weather in spring the water may be nearly 6° C. warmer than the air.

6. Phanerogamic vegetation is restricted to the lower reaches of the river, and poorly developed except in backwaters. In the upper reaches of the river the bryophyte vegetation is adequate, in the lower reaches bryophytes are very scanty. The algal flora is rich; *Lemanea* and *Stigeoclonium* are dominant types.

7. The fauna has been studied over a period of 9 months at five stations along the course of the river. Out of the 191 species which are recorded, 130 occur in the main-stream. Dominant animals are *Leuctra* spp., *Chloroperla* spp., *Baetis rhodani*, *Siphlonurus lacustris*, *Rhithrogena semicolorata*, *Heptagenia lateralis*, *Anabolia nervosa*, *Glossosoma boltoni*, *Mystacides azurea* and *Simulium reptans*.

REFERENCES

Berg, K. (1943). 'Physiographical studies on the River Susaa.' Folia Limnol. Scand. No. 1: 174 pp.

Butcher, R. W., Longwell, J. & Pentelow, F. T. K. (1937). 'Survey of the River Tees. Part III. The non-tidal reaches—Chemical and biological.' Tech. Pap. Water Pollution Res., Dep. Sci. Industr. Res. No. 6: 189 pp. London.

Butcher, R. W., Pentelow, F. T. K. & Woodley, J. W. A. (1930). 'Variations in composition of river waters.' Int. Rev. Hydrobiol. 24: 47–80.

Carpenter, K. E. (1924). 'A study of the fauna of rivers polluted by lead mining in the Aberystwyth district of Cardiganshire.' Ann. Appl. Biol. 11: 1–23.

Carpenter, K. E. (1927). 'Faunistic ecology of some Cardiganshire streams.' J. Ecol. 15: 33–54.

Carpenter, K. E. (1928). 'On the distribution of freshwater Turbellaria in the Aberystwyth district, with especial reference to two Ice-Age relicts.' J. Ecol. 16: 105–22.

Chandler, D. C. (1937). 'Fate of typical lake plankton in streams.' Ecol. Monogr. 7: 444–79.

Denham, S. C. (1938). 'A limnological investigation of the west fork and common branch of White River.' Invest. Indiana Lakes and Streams, No. 5: 17–71.

Eddy, S. (1932). 'The plankton of the Sangamon River in the summer of 1929.' Bull. Ill. Nat. Hist. Surv. 19: 469–86.

Embody, G. C. (1928). 'Stocking policy for the streams, smaller lakes and ponds of the Oswego watershed.' In 'A biological survey of the Oswego River system.' Suppl. to 17th Annu. Rep., State of N.Y. Conserv. Dep. pp. 17–39.

Fowler, W. W. (1887). 'The Coleoptera of the British Islands.' Vol. 1. London.

Frost, W. E. (1939). 'River Liffey Survey II. The food consumed by the brown trout (*Salmo trutta* Linn.) in acid and alkaline waters.' Proc. R. Irish Acad. B, 45: 139–206.

Frost, W. E. (1942). 'River Liffey Survey IV. The fauna of the submerged "mosses" in an acid and an alkaline water.' Proc. R. Irish Acad. B, 47: 293–369.

Galtsoff, P. S. (1924). 'Limnological observations in the Upper Mississippi.' Bull. U.S. Bur. Fish. 39: 347–438.

Hynes, H. B. N. (1940). 'A key to the British species of Plecoptera (stoneflies) with notes on their ecology.' Sci. Publ. Freshw. Biol. Ass. Brit. Emp. 2: 39 pp.

Ide, F. P. (1935). 'The effect of temperature on the distribution of the mayfly fauna of a stream.' Univ. Toronto Stud., Biol. Ser. No. 39: 3–76.

James, T. C. (1937). Minist. Agric. Fish. Standing Committee on River Pollution; West Wales Sub-Committee, Minutes of Meeting, 15 July 1937. Serial No. 779. London.

Jones, J. R. E. (1940). 'A study of the zinc-polluted River Ystwyth in North Cardiganshire, Wales.' Ann. Appl. Biol. 27: 368–78.

Jones, J. R. E. (1941). 'The fauna of the River Dovey, West Wales.' J. Anim. Ecol. 10: 12–24.

Jones, J. R. E. (1943). 'The fauna of the River Teifi, West Wales.' J. Anim. Ecol. 12: 115–23.

Jones, J. R. E. (1948). 'The fauna of four streams in the "Black Mountain" district of South Wales.' J. Anim. Ecol. 17: 51–65.

Kimmins, D. E. (1942). 'Keys to the British species of Ephemeroptera with keys to the genera of the nymphs.' Sci. Publ. Freshw. Biol. Ass. Brit. Emp. 7: 64 pp.

Kloet, G. S. & Hincks, W. D. (1945). 'A check list of British insects.' London.

Krogh, A. (1916). 'The respiratory exchange of animals and man.' London.

Laurie, E. M. O. (1942). 'The fauna of an upland pond and its inflowing stream at Ystumtuen, North Cardiganshire, Wales.' J. Anim. Ecol. 11: 165–81.

Laurie, R. D. & Jones, J. R. E. (1938). 'The faunistic recovery of a lead-polluted river in North Cardiganshire, Wales.' J. Anim. Ecol. 7: 272–89.

Murphy, H. E. (1922). 'Notes on the biology of some of our North American species of May-flies.' Bull. Lloyd Libr. Ent. Ser. No. 22: 1–46.

Murray, M. J. (1938). 'An ecological study of the invertebrate fauna of some northern Indiana streams.' Invest. Indiana Lakes and Streams, No. 8, 101–10.

Needham, P. R. (1928). 'A quantitative study of the fish food supply in selected areas.' In 'A biological survey of the Oswego River system.' Suppl. to 17th Annu. Rep., State of N.Y. Conserv. Dep. pp. 192–206.

Percival, E. & Whitehead, H. (1926). 'Observations on the biology of the mayfly, *Ephemera danica*, Müll.' Proc. Leeds Phil. Lit. Soc., Sci. Sect. 1: 136–48.

Pierce, E. L. (1947). 'An annual cycle of the plankton and chemistry of four aquatic habitats in Northern Florida.' Univ. Florida Stud., Biol. Sci. Ser. 4: 1–67.

Pyefinch, K. A. (1937). 'The fresh and brackish waters of Bardsey Island (North Wales): a chemical and faunistic survey.' J. Anim. Ecol. 6: 115–37.

Rawlinson, R. (1939). 'Studies on the life-history and breeding of *Ecdyonurus venosus* (Ephemeroptera).' Proc. Zool. Soc. Lond. B, 109: 377–450.

Reese, M. J. (1937). 'The microflora of the non-calcareous streams Rheidol and Melindwr with special reference to water pollution from lead mines in Cardiganshire.' J. Ecol. 25: 385–407.

Richardson, R. E. (1921). 'The small bottom and shore fauna of the middle and lower Illinois River and its connecting lakes, Chillicothe to Grafton: its valuation: its sources of food supply; and its relation to the fishery.' Bull. Ill. Nat. Hist. Surv. 13: 363–522.

Southern, R. & Gardiner, A. C. (1938). 'Reports from the Limnological Laboratory. IV. The Phytoplankton of the River Shannon and Lough Derg.' Proc. R. Irish Acad. B, 45: 89–124.

Thompson, D. H. (1925). 'Some observations on the oxygen requirements of fishes in the Illinois River.' Bull. Ill. Nat. Hist. Surv. 15: 423–37.

Welch, P. S. (1935). 'Limnology.' New York, etc.

Whitehead, H. (1935). 'An ecological study of the invertebrate fauna of a chalk stream near Great Driffield, Yorkshire.' J. Anim. Ecol. 4: 58–78.

Wiebe, A. H. (1927). 'Biological survey of the Upper Mississippi River with special reference to pollution.' Bull. U.S. Bur. Fish. 43: 137–67.

A LIMNOLOGICAL STUDY OF ERH HAI

2. BIOLOGICAL FEATURES

By SIDNEY C. HSIAO
Osborn Zoological Laboratory, Yale University, New Haven, Connecticut

1. INTRODUCTION

In a previous paper (Hsiao, 1946) the morphometry and the physico-chemical characteristics of the fresh-water lake Erh Hai in Yunnan, south-west China, have been reported. Since then the plankton material has been analysed both qualitatively and quantitatively, the bottom mud cores examined and some of the macrofauna and macroflora identified. A systematic account of the copepods has been given elsewhere. In this study the characteristics of the plankton, its seasonal variation and chemical composition, a short note on the macrofauna and macroflora and an account of the mud cores will be given.

2. METHODS

Collections of plankton were made at the surface layer between 1 and 2 m. (3–6½ ft.) and a deeper layer, between 3 and 5 m. (10–16 ft.). A regular plankton net 30 cm. in diameter was towed through the upper layer and a half-metre net of coarser mesh through the lower. As the locomotive power of the boat from which the nets were lowered was supplied by wind and human muscles, it was planned to tow the nets across the whole width of the lake, except at the beginning and the end of each trip when the boat would be in shoal water, so that the samplings made at different times of the year would be comparable. Theoretically the water filtered by a net as it is towed under water, if the size of the mesh does not change with towing time, equals the area of the net opening multiplied by the distance towed. In the case of a ½ m. net towed across the lake the volume of water filtered would be 1227·5 cu.m., and in the case of a 30 cm. net, 441·9 cu.m. But as the mesh opening is sooner or later reduced by the organisms caught on the net the actual value of water filtered is much less than the theoretical. Since the manner of this reduction of the mesh size varies with the occurrence of plankters which always appear in patches in a very irregular way, no simple correction is practical. This difficulty is aggravated in the case of a eutrophic lake. Apparently the data on total plankton catch in each instance are only a rough approximation: the higher values probably deviate more than the lower ones from what actually occurred in the lake.

Each plankton sample was fixed with formaldehyde as soon as it was transferred into a wide-mouth bottle. Owing to the limitation of equipment, no systematic collection of the limnoplankton from different strata of the lake was made.

To determine the total amount of plankton caught in each sample, a few aliquots of a well-mixed suspension was taken from each bottle to be dried to constant weight over a steam-bath and their dry weight recorded. The relative abundance of the common species of plankters was determined by examining their relative volume, after separation into species, in a well-mixed suspension of the total catch from each sample. By taking 1 ml. of the well-mixed plankton sample and diluting it to 10 ml., the number of individuals of the common species was counted with the help of a cross-grid ocular micrometer from several aliquots of 1 ml. each in a Sedgwick-Rafter counting chamber which has a volume of exactly 1 ml., and the number of individuals of each species was calculated in the usual way.

The total nitrogen of the zooplankton and phytoplankton was estimated separately on thoroughly dried material by the micro-Kjeldahl method as described by Boell (1945), except that saturated boric acid solution was used to absorb the ammonia distilled from the digest and later titrated against standard sulphuric acid using brom cresol purple as indicator. The total lipids were extracted from samples parallel to those used for total nitrogen estimation by the rapid micro-method described by Hsiao (1948). The alcoholic extracts were evaporated to dryness under a stream of CO_2 and taken up with diethyl ether. This portion and the ether extracts were combined, dried under CO_2 to constant weight, and the percentage of the extract calculated.

3. TOTAL TOW-NET PLANKTON

There are two maxima in the total dry weight of the plankton collected monthly during the year 1944–5. The first increase in quantity occurs in the fall when the water temperature of the lake was decreasing (Fig. 1), as observed by West in the English Lake

District (West & West, 1909; West, 1916) and later reported from other lakes by different observers. A second maximum occurs in March and April. There is a clear minimum in August and a less striking one in February. This appears similar to the situation observed in Lake Mendota, though in the latter case the February minimum is the most striking one (Birge & Juday, 1922). The quantitative change in plankton crop seems to be related to three environmental factors in Lake Erh Hai. First, the temperature: a striking increase is seen at the time when the mean temperature of the water is decreasing. This agrees with the conclusions of Lemmermann (1903, 1908) and West (1916), and many others. Secondly, the weather: the south-western part of the Yunnan plateau has a semi-tropical climate with its rainy season controlled by the monsoon from the Indian Ocean. The drainage is greatly increased and the turnover of water through the lake is very great during the rainy season, but very small during the dry period of the year. Lu (1939), in his study of the Cladocera of this lake, was the first to point out that the rainy season is the less productive period in this lake. The striking minimum in the total dry weight of tow-net plankton in August takes place at the time when the current running through the lake is at its height. Thirdly, human interference: this lake is one of those which is fertilized artificially, though unconsciously, by man, for all the available land on both sides of this elongated lake is intensively cultivated and the practice of flooding the dry fields at the beginning of the rice planting season, the maintenance of irrigation during the growth of the crop and the draining of all the rice paddies at harvest time all help to carry down to the lake fertilizers placed in the fields by the farmers. This agricultural fact is perhaps very important in making Lake Erh Hai eutrophic. The second maximum in the total dry weight of plankton occurs around April, at a time, in contrast to the first maximum, when the water temperature is not decreasing, but gradually increasing. Other factors are probably at work which may be more effective than temperature alone. This is the time when the leguminous crops, *Vicia faba* L., *Glycine soja* (S. and Z.) and *Pisum sativum* L. are being harvested, the soil ploughed up and flooded in preparation for the planting of rice (*Oryza sativa* L.). This is at the end of the dry season. The level of the lake is low, the transportation of water out of the basin very small and fertilizers are added to the lake through cultural activities—all these may work together to provide a favourable environment for the increase of plankters in the lake. On the other hand, during the summer rainy months, although there is a continuous supply of fertilizers, the amount varies from time to time, the rapid transport of water in torrents down the steep high mountains on the two sides of the lake besides introducing tychoplankton (heleoplankton) and potamoplankton, also washing out the limnetic population from the lake—it does not favour the increase of limnoplankton. It is doubtful if there is a depletion of nutrients by the abundant growth of limnoplankton in April and May, for the allochthonous supply may be able to counterbalance it. Data on the chemistry of the nutrient content of the lake water would be highly desirable.

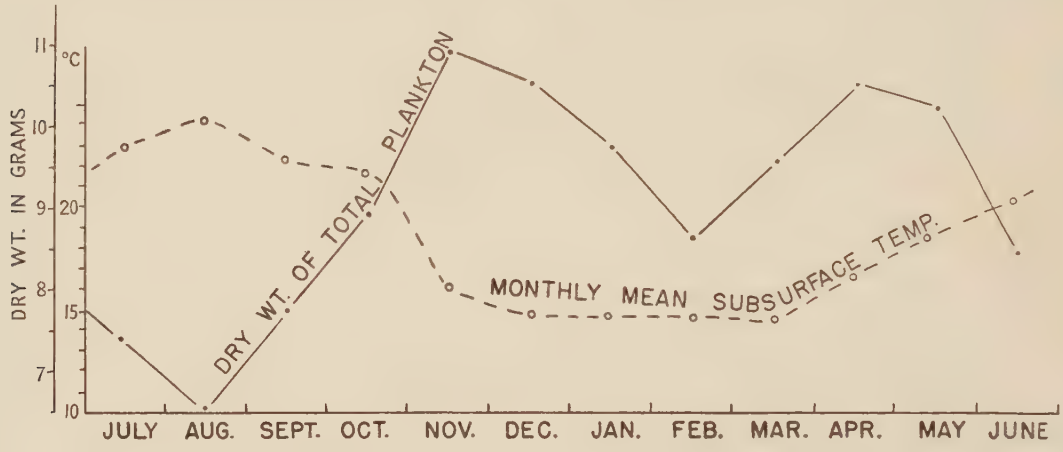


Fig. 1. Monthly total plankton catch and mean subsurface temperature of Lake Erh Hai.

4. ZOOPLANKTON

The zooplankton in this lake is dominated by copepods. A list of the zooplankters contains the following forms:

PROTOZOA
- Arcella vulgaris Ehr.
- Difflugia sp.

*CLADOCERA
- Daphnidae
  - Daphnia longispina var. hyalina Sars
  - Scapholeberis mucronata (O.F.M.)
  - Simocephalus vetullus (O.F.M.)
  - Ceriodaphnia quadrangula (O.F.M.)
- Bosminidae
  - Bosmina longirostris (O.F.M.)
- Chydoridae
  - Alona costata Sars
  - A. guttata Sars
  - A. rectangula Sars
  - Graptoleberis testudinaria (Fischer)
  - Alonella excisa (Fischer)
  - Pleuroxus aduncus (Jurine)
  - Chydorus ovalis Kurz
  - C. sphaericus (O.F.M.)
  - Anchistropus emarginatus Sars
- Leptodoridae
  - Leptodora kindtii Lilljeberg

COPEPODA
- Diaptomidae
  - Tropodiaptomus hebereroides Hsiao
  - Arctodiaptomus hsichowensis Hsiao
- Cyclopidae
  - Eucyclops serrulatus extensus Hsiao
  - Tropocyclops breviramus Hsiao
  - Megacyclops viridis (Jurine)
- Argulidae
  - Argulus japonicus Thiele

* This list of Cladocera is largely based on Lu's (1939) work on the Cladocera of Lake Erh Hai.

plankton is at a maximum. The number of individuals counted in 1 c.c. with a Sedgwick-Rafter counting chamber for each species is given for each month. It will be seen that the most common species are *Leptodora kindtii, Daphnia longispina, Tropodiaptomus hebereroides, Arctodiaptomus hsichowensis* and the immature stages of cyclopoids.

The relative volumes occupied by these common plankters are shown in Table 2, which gives an

Table 1. *Number of common zooplankters from tow-net catches in 1 c.c. of well-mixed suspension, estimated by Sedgwick-Rafter counting method*

Animals	Nov.	Dec.	Apr.
*Leptodora kindtii**	210	310	180
Daphnia spp.	140	50	180
Tropodiaptomus hebereroides, ♂♂	200	150	140
T. hebereroides, ♀♀	150	130	130
Arctodiaptomus hsichowensis, ♂♂	120	120	110
A. hsichowensis, ♀♀	70	80	90
Eucyclops serrulatus extensus	20	10	20
Megacyclops viridis	10	5	0
Immature diaptomids	60	40	80
Immature cyclopoids	30	80	120

* As *Leptodora kindtii* are very fragile, usually broken up into fragments in the samples, and as they have a tendency to float on top of the other plankters, making even mixing of the catches for sampling difficult, the figures for this species may be too high.

Table 2. *Settled volume of the commonest zooplankters in 20 c.c. of plankton collected from Lake Erh Hai*

Group or species ...	*Leptodora kindtii*	*Argulus japonicus*	Calanoida	Cladocera	Cyclopoida	Others
Settled volume in c.c.	10	7	2	0·5	0·4	0·1
Percentage of total	50	35	10	2·5	2	0·5

Brehm (1924) described a diaptomid copepod, *Diaptomus bidens* and a harpacticoid, *Handeliella paradox* from this lake. But Pesta (1930) showed that the harpacticoid belongs to the same genus as Sars' *Harpacticella* named in 1908. It is obvious that many species of Protozoa may have passed through the plankton net and hence not been found in the samples collected. The rotifer fauna appears to be very poor. Among the tow-net plankton, Cladocera and Copepoda dominate the catches both in volume and in number of individuals. The relative abundance in number of these zooplankters is given in Table 1, where the samples consist of 1 c.c. of well-mixed suspension from catches made in November, December and April when the total dry weight of the approximate estimation of each species from among 20 c.c. of settled plankton.

The abundance of *Leptodora* may be actually less than the figures indicate, because it is relatively lighter than the other species and it is not easy to distribute the individuals evenly among the other forms, so that when an aliquot is taken more of this species might be drawn from the surface of the sample in the bottle.*

* At the time when this survey was made there were no facilities for separating the species for systematic determination. Upon transporting the material from south-west China over the Stilwell Road to the Yangtze valley a serious accident involving the overturn of a truck destroyed most of the plankton samples and the fish and bird specimens. It is now impossible to obtain an idea of the total catch of each species among the most common forms throughout the year.

5. PHYTOPLANKTON

The phytoplankton is characterized by the predominance of Myxophyceae so that it appears as a 'blue-green soup' (Dr Patrick's term) in the preservation bottle. But the number of species is very small. The most abundant phytoplankters are: *Aphanizomenon flos-aquae* Bornet & Flahault and *Diplocystis aeruginosa* (Kürtz) Trevis.

Aphanizomenon flos-aquae, one of the common Nostocaceae, is most abundant in summer and autumn. During their bloom, these algae are very thick and aggregate into bundles so that the water looks yellowish and appears filled with chopped hay glittering in the sunlight. The Chroococcaceaen, *D. aeruginosa*, is most frequently seen in the winter months. When this species dominates the phytoplankton, deep blue-green floating clusters are formed that give a decided colour to the surface water as observed by Lemmermann (1903) in Lake Plön and by West & West (1916) in Irish lakes. This Myxophyceae bloom is a very noticeable phenomenon in this lake.

The diatoms are scarce both in number of species and in the number of individuals in each species. *Stephanodiscus* sp.nov. is more numerous than all the other diatoms, though compared with the other plants and animals its total quantity is small. This species is being described by Dr R. Patrick and will be published in *Notulae Naturae* of the Academy of Natural Sciences of Philadelphia. The digestive tract of *Tropodiaptomus hebereroides* seems to concentrate this species of diatom.

The following phytoplankters are found in the water of Lake Erh Hai:

MYXOPHYCEAE
- Chroococcaceae
  - Diplocystis aeruginosa (Kütz) Trevis
- Nostocaceae
  - Anabaena sp.
  - Aphanizomenon flosaquae Bornet & Flahaut
- Oscillatoriaceae
  - Oscillatoria sp.

BACILLARIACEAE
- Coscinodiscaceae
  - Melosira granulata (Ehr.) Rolfs, Stephanodiscus sp.*
- Achnanthaceae
  - Cocconeis placentula var. euglypta (Ehr.) Cl.
  - C. pediculus Ehr.
- Cymbellaceae
  - Cystopleura sorex (Kütz) Kunz
  - C. zebra var. saxonica (Kütz) Kunz

CHLOROPHYCEAE
- Hydrodictyaceae
  - Pediastrum simplex Meyer
  - And a few other unidentified species

DINOPHYCEAE
- Peridiniaceae
  - Ceratium hirundinella O.F.M.

With the exception of *Diplocystis aeruginosa* and *Aphanizomenon flos-aquae*, there is on the whole a paucity of limnotic species of phytoplankton, and the number of individuals is also small in most species. This is especially true with respect to diatoms. But among littoral plants the attached species of diatoms are rather abundant.

6. CHEMICAL COMPOSITION OF TOW-NET PLANKTON

Chemical analyses show that on the average, each ml. of settled zooplankton contains 105·8 mg. of wet material. Of the wet material 91·2% consists of water and substances volatile at 100° C., that is, about 9·1 mg. of dry matter is contained in each ml. of settled zooplankton. A typical series of analyses is shown in Table 3.

Table 3. *Wet weight, dry weight and ash content of zooplankton*

Settled volume (ml.)	Wet wt. (g.)	Wet wt. per ml. plankton	Water (%)	Dry wt. (mg.)	Dry wt. per ml. wet plankton	Ash (%)
21	2·221	106·76	91·2	194·6	9·27	7·08
12·5	1·318	105·46	91·2	113·7	9·1	6·8
18·0	1·909	106·04	91·1	162·1	9·0	7·4
Av.		105·75	91·2	—	9·1	7·1

Zooplankters dried to constant weight were used for the estimation of total nitrogen, total carbon and lipid extractives, and the three types of material, protein, fat and carbohydrate, calculated with the usual method. On the average, 9·8% of dry zooplankton material is nitrogen, which, when multiplied by a factor of 6·25, as done by Birge & Juday (1922, 1934) gives 61·2% 'crude protein'. There are 17·9% of the dry material extractable with lipid solvents. The rest consists of crude carbohydrate. As the zooplankton consists mainly of *Leptodora*, *Diaptomus*, Cyclopoids and *Daphnia*, it is of interest to compare its chemical composition with the determinations made on these organisms by Birge & Juday. In the following table, Table 4, the 1922 data of these authors are compared with the material from Lake Erh Hai.

It will be seen from this table that the values of the main chemical constituents of the zooplankters of Lake Erh Hai fall within the range found for those of

Table 4. *Chemical composition of various plankton organisms in percentage of dry weight of sample*

Source of material	Samples used	Organisms	Total nitrogen Mean	Total nitrogen Range	'Protein' (N × 6·25) Mean	'Protein' (N × 6·25) Range	Lipid extractives Mean	Lipid extractives Range	Ash Mean	Ash Range
Lake Mendota	4	*Diaptomus Cyclops*	9·57	9·27–9·87	59·81	57·93–61·69	18·07	16·74–19·80	5·71	5·58–5·82
Devils Lake	5	*Daphnia pulex*	7·09	5·82–8·27	44·31	36·38–51·69	5·3	2·82–12·07	22·0	16·87–25·85
Lake Monnona	3	*Daphnia pulex*	8·35	7·91–8·63	52·19	49·44–53·19	11·04	3·45–21·25	13·49	7·62–18·21
Lake Monnona Lake Mendota	2 1	*Leptodora*	8·94	7·69–9·84	55·85	48·06–61·50	13·50	5·88–25·93	11·94	8·00–15·50
Lake Erh Hai	3	Zooplankton	9·8	—	61·2	—	17·9	—	7·1	—

Table 5. *Wet weight, dry weight and ash content of phytoplankton*

Wet wt. (mg.) per ml. settled volume	Percentage of water	Dry wt. (mg.) per ml. settled volume	Ash (% dry wt.)
251·6	89·86	25·36	4·7
247·6	90·13	24·9	4·9
243·6	89·57	24·44	5·4
Av. 247·6	89·85	24·9	5

Table 6. *Chemical composition of various phytoplankton organisms as percentage of dry material*

Samples used	Organisms	Total nitrogen Mean	Total nitrogen Range	Protein Mean	Protein Range	Lipid extractives Mean	Lipid extractives Range	Ash Mean	Ash Range
7	Erh Hai phytoplankton	7·0	—	42·74	—	6·96	—	5·0	4·7–5·4
3	*Microcystis*	8·06	6·32–9·27	50·4	39·5–57·94	3·32	2·67–4·55	5·62	4·31–7·54
2	*Aphanizomenon*	9·62	9·3–9·94	60·12	58·12–62·12	4·03	3·72–4·34	7·02	6·52–7·51

Copepods and Cladocera from the Wisconsin lakes. There is less ash in the Erh Hai material, and the proportion of nitrogenous material and lipid extractives falls on the higher side of the Wisconsin figures.

Compared with zooplankton, the phytoplankton has relatively less settled volume, that is, it contains more material per volume of organism: expressed on a unit settled volume basis, the phytoplankters weigh 2·3 times as much as the zooplankters, and contain 2·7 times as much dry matter as well as organic matter as the latter. Expressed in terms of wet weight, the phytoplankters contain 89·85 % water and substances volatile at 100° C. against 91·2 % for zooplankters. These facts are shown in Table 5.

Dried phytoplankton consists of 42·7 % 'crude protein', 6·96 % lipids and 50·3 % carbohydrate and related material. In Table 6 the data from analyses of two species of Myxophyceae made by Birge & Juday on Lakes Mendota and Monnona material are reproduced below those from Erh Hai phytoplankton. It will be seen that, generally speaking, the phytoplankton from Erh Hai, which is largely *Aphanizomenon* and *Diplocystis* (=*Microcystis*), have lower nitrogen and ash content but higher lipid extractives. The value for nitrogen, however, falls within the range of the Wisconsin material, but that of the lipids are outside the range of their Myxophyceae but less than their value (Birge & Juday, 1934) for diatoms from sixteen analyses of south Wisconsin lakes.

7. TOTAL SOLID RESIDUE FROM LAKE WATER

As tow-net catches will only give a partial picture of the total crop of a lake, being inaccurate in sampling the density of limnoplankton populations, and retaining a small but variable amount of nannoplankton, and because no dissolved organic matter can be sampled by nets, water samples from the surface of the lake from west to east were taken in the months of November, December and January, when the weather was calm during this windy season, and the plankton growth at a maximum. The figures in the third column of Table 7 represent weights of solid residue minus substances volatile on steam-bath, from 100 ml. samples of surface water calculated to mg./l. It will be seen that along the littoral region, particularly among rooted plants, the solid contents on both sides of the lake are very high. But at one-third to one-half the way across the lake there are 139–176 mg. solid material per litre of water—less than half the high values along the littoral region. There is a good deal of gravel and other detritus stirred up by wave action along the shore. In the middle portion of the lake there is, on the average, 159 mg. of solid residue per litre of water.

Table 7. *Total solid residue of lake water after evaporation*

Date	Distance off shore	mg./l. solid residue	Remarks
November	Littoral	325	Among rooted plants
	1 mile	280	—
	6 miles	176	Half way across
December	Littoral	301	—
	2 miles	272	—
	5 miles	139	—
January	Littoral	343	East side of lake
	Littoral	257	West side of lake
	½ mile	236	East side of lake
	2 miles	159	—
	6 miles	163	—

In their survey of 529 lakes in the northern lake region of Wisconsin, Birge & Juday (1934) gave 10–110 mg./l. of water as the range of total solid residue and a mean value of 15·8 mg./l. for drainage lakes. It seems that Erh Hai has higher residue than any of these Wisconsin lakes.

If, for purposes of comparison, the total organic matter is assumed to be about the same as those proposed for the Wisconsin lakes, it appears that the standing crop of Lake Erh Hai, when computed from the volume of the lake, is higher than what Birge & Juday found for their lakes.

8. MACROFAUNAL AND MACROFLORAL FEATURES

Lake Erh Hai is rich in macrofauna and has a useful macroflora. With its economic products this lake supports one industry which gives full-time employment and several part-time occupations for the inhabitants of the Tali valley.

From the macrofauna of Erh Hai collections of Porifera, Mollusca, Arthropoda, fish and birds were made.

Fresh-water sponges are fairly abundant in this lake. Chang & Chen (1947), who studied the fresh-water sponges of Yunnan, reported three species from Lake Erh Hai, namely, *Ephydatia fluviatiles* (Auct.), *Trochospongilla latouchiana* (Annandale), and *Nudospongilla coggini* (Annandale).

Mollusca are represented by several species of Gastropoda and one species of Lamellibranch. These are:

GASTROPODA
- Viviparidae
  - Viviparus chinensis ventricosus Heude
  - V. chinensis Gray
  - Margarya melanoides Nevill
- *Pleuroceratidae
  - Fenouilia bicingulata Heude
  - Paraprososthenia gredleri (Neumayer)
  - P. coggini Annandale & Prashad

LAMELLIBRANCHIA
- Cyrenidae†
  - Corbicula fenouilliana Heude

Heude (1889) also described *Delavaya rupicolor* from this lake. Apparently *Fenouilia kreiteri* (Neumayer) of Annandale and Prashad, *Lithoglyphus kreiteri* var. *carinata* and var. *bicarinata* of Neumayer and *Jullienia carinata* of Fulton are synonymous with *Fenouilia bicingulata*.

Among molluscs *Margarya melanoides* is the most abundant living form. It is distributed from the littoral to the sublittoral zone in this lake. Outside this basin it is also found in Kien Chuan valley, approximately 100 miles to the north and connected with this lake by a number of water courses. Fossil forms of this species have been reported from Kunming, about 300 miles to the south-east (Yang, 1930) but geological data were lacking. *M. melanoides* is apparently an endemic species of this part of the country and has not been reported from elsewhere. It has the superficial characters of sea-shells. The thick columnar layer is covered by a thin periostracum

* Annandale & Prashad (1919) proposed placing these two genera in the family Pleuroceratidae, but Thiele (1931) placed them in the subfamily Hydrobiinae of the family Hydrobiidae.

† Thiele (1931) substituted Corbiculidae for this name whose type genus *Cyrena* has been proved to be synonymous to *Corbicula*.

which is clean and smooth. Robust individuals carrying heavy spinous processes are as common as the more smooth ones. The sculpture, solidity, and un-encrusted appearance of the shell recall the 'thalassoid' genera of Tanganyikan Melaniidae. (Pilbry & Bequaert (1927, pp. 581–95) gave an interesting discussion on the use of this term for some of the endemic genera of molluscs in Lake Tanganyika.) The radiating spines on the shell remind one of those of *Tiphobia* of Lake Tanganyika.

Viviparus chinensis is a widely distributed species in China. In many parts of central and eastern China it occurs in such abundance that it is sold in the market for food. In this basin the number of individuals of this species is too small to be worth fishing. None of the other gastropods listed has been reported from other places. No living specimens of *Paraprososthenia gredleri* has been observed, although the supralittoral zone has countless layers of empty shells of this form. Fragments of this species have been found in the mud cores from the lake bottom. High up in the valley on the west side of the lake and scattered over the alluvial plain, many beds of *Paraprososthenia* and *Margarya* shells are seen. *Corbicula fenouilliana* inhabits the shallower portion of the littoral zone and it is less numerous than the gastropods.

Among the Arthropoda, the fresh-water shrimp, *Palemon* sp. is caught and sold for food. But the quantity is so limited that the small catches are generally dried and sold in the grocery shops as flavouring material for soup. There is a very rich fauna of insect larvae. The most prominent forms are Ephemerid larvae, Chironomid larvae, Zygoptera and Anisoptera imagines and nymphs. Kieffer (1911) described five species of Chironomids (Tendipedidae) from western Yunnan: *Tendipes atrifurca, T. sinensis, T. browni, Tanytarsus sinarum, Pelopia callicoma*. The other benthic arthropod material was lost during transportation out of Yunnan. The Hydrachnids were lost in the mail while being sent to Dr Viets at Bremen for identification.

Of the fishes found in Lake Erh Hai the Cyprinidae form the most numerically important group. The common species are *Cyprinus carpio* L., *Carassius auratus* (L.) and *Schizothorax taliensis* Regan. The following species are among those found in this lake:

CYPRINIDAE
- Cyprininae
  - Cyprinus hybiscoides Richards
  - C. carpio L.
  - C. auratus (L.)
  - Schizothorax progastus (McClelland)
  - S. taliensis Regan
  - Labeo yunnanensis Chaudhuri
  - Barbus cogginii Chaudhuri
  - Barilius polylepis Regan
- Cobitidinae
  - Misgurnus anguillicaudatus (Cantor)
  - Nemachilus pleurotaenia Regan

SILURIDAE
- Bagrinae
  - Macrones seenghala (Sykes)

OPHIOCEPHALIDAE
- Ophiocephalus gahua Ham Buch.
- O. punctatus Bloch

As the greater part of our extensive collection of fishes was lost on the way over the Stilwell Road it is not possible to say whether new species were included among the material.

Through the help of Dr Taylor of the Education Department who did the shooting, a large number of bird skins were secured. These bird skins were all lost in the truck accident when they were being transported out of Yunnan.

Herbarium specimens of the macroflora collected from this lake were identified by Dr Merrill. The common species are:

PTERIDOPHYTA
- Marsileaceae
  - Marsilea quadrifolia L.

SPERMATOPHYTA
- Monocotyledonae
  - (*a*) Hydrocharitaceae
    - Vallisneria spiralis L.
    - Hydrilla verticillata Royle
    - Xystrobolus yunnanensis Gagnep
  - (*b*) Potamogonaceae
    - Potamogeton malainus Mig.
    - P. perfoliatus L.
    - P. crispus L.
  - (*c*) Najadaceae
    - Najas major Allioni
  - (*d*) Pontederiaceae
    - Eichornia crassipes Solms
  - (*e*) Cyperaceae
    - Scirpus sp.
  - (*f*) Gramineae
    - Echinochloa crus-galli (L.) Beauv. var.
    - Phragmites communis Trin.
    - Panicum (possibly) sp.
- Dicotyledonae
  - (*a*) Crucifereae
    - Cardamine sp.
  - (*b*) Polygonaceae
    - Polygonum glabrum Willd.
    - P. barbatum L.
    - P. amphibium L.
    - Polygonum sp.
  - (*c*) Onagraceae (Oenotheraceae)
    - Trapa natans L.
  - (*d*) Halorrhagaceae
    - Myriophyllum verticillatum L.
  - (*e*) Gentianaceae
    - Nymphoides peltatum (Gmel.)

9. ECONOMIC USE OF THE MACROFAUNA AND MACROFLORA

The larger forms of plants and animals are utilized in the following: fishing industry, snail fishing, as game birds, as food plants and plant fertilizers.

The fresh-water fishery, though conducted along very primitive lines, gives employment to a number of villages along the side of the lake. Seine nets, dip nets and various types of fish traps are used in the open water. Cormorants are used a good deal in the shoal water, while specially constructed traps are employed exclusively at the entrance of estuaries to catch fishes during their breeding migrations. The most common fishes caught for the market are carp, wild-type goldfish and 'bow fish' (*Schizothorax taliensis*). The last species is considered a speciality of this lake and is caught in large quantity during the spawning season in September and October at the entrance of the estuaries. A good number of carp as large as 2–3 ft. in length and weighing 40–50 lb. are often brought to the market for sale. Fingerlings are ruthlessly caught and sold in quantity. In certain arms and bays of the lake pisciculture of sorts is practised. It is generally limited to providing nesting grounds and throwing fresh leaves on top of the water.

The viviparous snail, *Margarya melanoides*, is also an important economic product of this lake. At the present time several hundred kilograms of snails are fished every day for sale in the local market in the valley. Fishing for this snail is an all-year-round industry which gives support to a number of families at the lake shore. The snails are either sold in the shell or, more generally, shelled and the ovaries sold separately from the rest of the soft tissues. This snail fishing industry has apparently been developed for a great many years. In the first place, the extensive piles of empty shells concentrated on different points along the shore of the lake indicate that the amount of snails shelled has been enormous. In the second place, the scattered beds of *Margarya* shells which, according to geologists, indicate that possibly the shore line was at one time much nearer to the foot of the mountain, may also be an indication of the extensive use of this species by the earlier inhabitants of this valley just as they are being shelled to-day on the present lake shore.

Birds feeding on Lake Erh Hai have been shot, particularly during the winter months, by local fowlers with old-fashioned long barrel shot guns. Ducks and water fowl are the most important marketable birds while the Herodiones and Gaviae, though present in large numbers, are not molested.

The aquatic plants from this lake are either used as food or gathered for fertilizers. *Xystrolobus yunnanensis* is an economically important plant in the Tali Valley. It is harvested in the spring when the flowers are in bud. Small flat-bottomed boats equipped with a bamboo pole with a hook at the end, or with two pieces of bamboo poles 8–12 ft. long, tied together in the form of a letter 'X' are dragged through the littoral zone of the lake, pulling the flowering stalk up as far down toward the root as possible. Such flowering stalks are arranged side by side on board the boat across the bow. On preparing for the market, bundles of 1–2 in. in diameter, consisting of 20–40 plants, are braided together into disks and sold as a vegetable under the name of 'sea-weed'. When used as food, the stalks are partially skinned, cut into sections of about 1 in. in length and made into soup which has a thin gelatinous consistency. It is customary to boil these plants with pork and seasoning.

The fruit of *Trapa natans* is collected in May and June and sold in small quantities on the market. Since the quantity is small, it is not made into flour as is done in India and some parts in the lower Yangtze Valley. It is only used as a fruit.

Myriophyllum verticillatum is a favourite of gardeners and fish fanciers. It is much used as a decorative plant in gold fish bowls and ponds all over China. This species is occasionally taken from the sheltered bays of Lake Erh Hai for this purpose.

For fertilizing their fields littoral plants, both attached and floating, are indiscriminately gathered three times a year and left to dry on the shore by farmers who have fields near the lake. Dried plants are scattered in the fields, but occasionally they are burned in the field and their ashes scattered later. Except for what is washed out of the lake during the rainy season, the method of cultivation and utilization of the lake keeps the nutrients in a nearly closed cycle year after year.

10. LAKE SEDIMENTS

Samples of lake sediments were obtained by means of a core sampler built upon the principle described by Jenkin & Mortimer (1938) and Jenkin, Mortimer & Pennington (1941). Owing to the lack of building materials, the longest core obtained was only 1·5 m. (4·9 ft.) in length. After drying to constant weight, a selection from different sections of the core was subject to chemical analyses by methods adopted in Prof. Hutchinson's laboratory at the Osborn Zoological Laboratory. Iron and titanium were estimated volumetrically after precipitation with cupferon, the other ions were determined with methods given by Hillebrand & Lundell (1929). The diatoms in the sediment were cleaned with the acid method used in Dr Patrick's laboratory, the mud sample being boiled with HNO_3 followed by $K_2Cr_2O_7$ and later washed clean with distilled water until colourless and neutral, using a centrifuge to retain the solid remains from the oxidation treatment. The size of particles from several layers in the sediment was analysed by the sedimenta-

tion method described by Krumbein & Pettijohn (1938). Corresponding samples of mud were examined under the microscope for pollen grains and other microfossils.

None of the cores collected with the sampler reached beyond a material which may be termed the 'brown mud'. Dr Patrick, who examined the material for diatoms, found the following species, all of which were of rare occurrence:

Stephanodiscus spp. nov. (to be described by Dr Patrick), more abundant than the other species
Melosira granulata (Ehr.) Rolfs
M. granulata v. augustissima Müll
M. distans v. alpigena Grun
Fragilaria construens v. venter (Ehr.) Grun
F. pinnata Ehr.
F. pinnata v. lancettula (Schum.) Hust.
Cocconeis placentula Ehr.
Caloneis silicula (Ehr.) Cl.
Navicula scutelloides W-Sm.
Cytopleura sorex (Kütz) Kunze
C. zebra v. saxonica (Kütz) De-toni

It will be seen from this table that samples A_{17} and A_{31} are similar to each other but differ from the others in that: (1) their median values are 6·6 and 6·7 ϕ units instead of greater than 7 as in the other samples (7·2 to 7·9); (2) these two samples, as shown by quartile deviations, are less spread in their cumulated frequency curves than the others: only three Wentworth grades between quartiles, whereas the others have four or more; (3) the quartile skewness indicates that none of the curves is symmetrical, but the arithmetical means of the quartiles for samples A_{17} and A_{31} are half or a third Wentworth grade to one side of the median while all the others are skewed the other way; (4) by Trask's standards, samples A_{17} and A_{31} are better 'sorted' than the others, as shown in the last column in Table 8. Smaller spread in particle size in the sediment of an open lake may indicate that during the time when these two layers were deposited the source of the silt was more uniform.

The results of chemical analyses are set forth in Table 9. The total ash content of the samples analysed

Table 8. *Statistical parameter based on mechanical analysis of bottom sediment from Lake Erh Hai*

Layer	Depth (cm.)	Median (Md_ϕ)	Spread (Q_1–Q_3)	Quartile deviation (QD_ϕ)	Quartile skewness ($Sk_{q\phi}$)	Trask's sorting coefficient (S_ϕ)
A_1	2	7·9	4·8	2·4	−0·25	5·25
A_5	15	7·2	4·0	2·0	−0·3	4·0
A_{11}	36	7·4	4·2	2·1	−0·5	4·25
A_{17}	56	6·7	2·9	1·45	+0·55	2·75
A_{25}	80	7·8	4·0	2·0	−0·5	4·0
A_{31}	100	6·6	3·0	1·5	+0·35	2·85

Table 9. *Inorganic constituents of bottom sediment of Lake Erh Hai*

Sample	Depth (cm.)	Loss on ignition	SiO_2	Fe_2O_3	Al_2O_3	P_2O_5	TiO_2	MuO	CaO	MgO
A_2	2·2	11·90	54·45	1·15	19·92	0·19	1·95	0·68	2·93	5·24
A_6	15	13·08	53·75	1·97	21·12	0·12	1·41	0·52	2·45	4·41
A_{16}	55	11·39	47·86	1·19	26·27	0·08	1·41	0·75	5·21	4·81
A_{20}	66	10·85	57·35	1·02	20·81	0·11	1·59	0·35	2·21	4·24
A_{25}	80	11·45	49·14	1·03	24·19	0·07	1·40	0·50	5·11	6·03
A_{29}	89	11·86	46·46	1·21	25·11	0·21	1·40	0·13	5·78	6·80

The scanty material makes it impractical to study the vertical distribution of diatom remains in the bottom sediment of this lake. It is probable that the total silica content of the bottom mud is not influenced by the distribution of diatoms in the different layers. The only type of pollen observed from the cores seems to belong to a species of walnut.

The results of mechanical analyses are represented graphically according to the method of Krumbein (1939) in Fig. 2, where the cumulated frequencies of each sample from top, layer A_1, to the bottom, A_{31}, are plotted against ϕ, as independent variable. From these graphs the usual statistical parameters are taken and summarized in Table 8.

varies from 88·1 to 89·2 % of the dried sediment. It is higher than that from Linsley Pond found by Hutchinson & Wollack (1940). Compared with the material from Tibetan lakes studied by Hutchinson, Wollack & Setlow (1943), it is seen to be less than those of the open lakes but more than the closed ones, a condition which is to be expected, for in mountainous regions where there is scanty forestation silt brought into the basin forms the most important portion of the inorganic deposit. Nevertheless, the low loss on ignition is remarkable for so eutrophic a lake. Either very rapid silting or intense bacterial decomposition, or both, must be contributing to keep the organic fraction at a low level.

The calcium content in the sediment is the most interesting point in the analytical results. It exhibits two maxima, one in sample A_{16} from a depth of 55 cm. below the bottom of the lake and the other in sample A_{29} from 89 cm. They are associated with corresponding increase in magnesium content. This condition, when considered together with the facts from particle size analyses, which show that the particles of the layers corresponding to these maxima are coarser and have less 'spread' (better sorted in Trask's sense), suggests that during the time when these two layers were deposited the weather was drier and the lake level lower, perhaps not reaching the outlet with resulting greater precipitation of calcium and magnesium salts. Between the time of these two deposits a wetter period intervened. Since the sedimentary samples collected are short and since no time scale can be constructed from the available data, no other climatological interpretation besides this deduction can be profitably advanced.

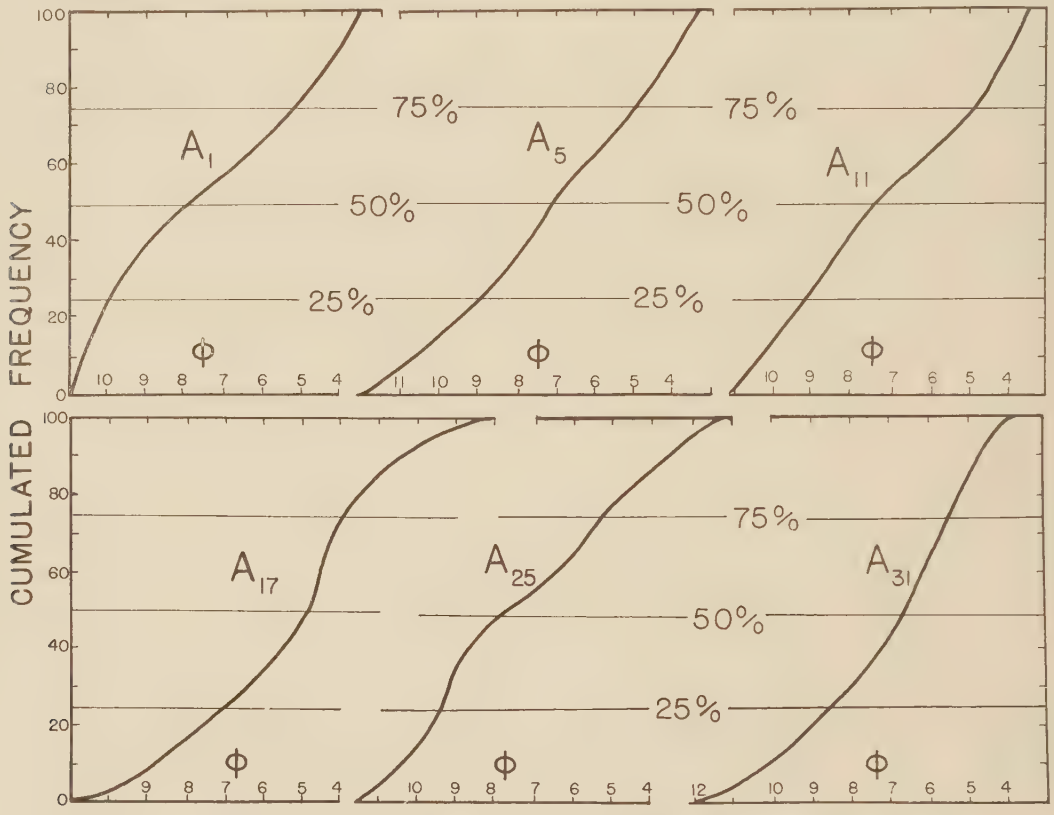


Fig. 2. Cumulative curves from mechanical analyses of bottom sediment of Lake Erh Hai.

II. SUMMARY

1. The total quantity of tow-net plankton from Lake Erh Hai shows two maxima: one occurs between November and December, and the other, March and April. The first is associated with a fall in the mean temperature of the water and the second with the end of the dry season. There is a pronounced minimum in August and a less striking one in February. The relation between total plankton quantity and the effect of water temperature, weather conditions and cultural interference is discussed.

2. Quantitatively the most prominent zooplankters are Cladocera and Copepoda. Among the former, four species of Daphnidae, one species of Bosminidae, nine species of Chydoridae and one species of Leptodoridae are found. Two species of Diaptomidae, three species of Cyclopidae and one species of Argulidae are found among the Copepoda. Of these six species, two diaptomids and two cyclopoids are new. The most common species occurring during the plankton maxima are *Leptodora kindtii*, *Daphnia longispina*, *Tropodiaptomus hebereroides*, *Arctodiaptomus hsichowensis* and the immature stages of cyclops and diaptomids.

3. The most abundant phytoplankters are *Aphenizomenon flos-aquae* and *Diplocystis aeruginosa* which form the bulk of 'Myxophyceae bloom'. There are

two species each of Coscinodiscaceae, Achnanthaceae and Cymbellaceae. There is a paucity in the number of species and individuals of each species of diatoms in the open water.

4. Each ml. of settled zooplankton contains 105·8 mg. of wet matter of which 91·2% consists of water. About 9·1 mg. of dry matter is found in each ml. of settled zooplankton. On the average 9·8% of dry zooplankton is nitrogen, giving a 'crude protein' value of 61·2%; 17·9% is lipid and the rest 'crude carbohydrate'. Phytoplankton contains 89·8% water and each ml. of settled material contains 24·9 mg. dry matter, of which 42·7% is 'crude protein', 6·9%, lipid, and 50·3% 'crude carbohydrate'. These values from chemical analyses have been compared with those found by Birge & Juday in Wisconsin lakes.

5. Among the macrofauna the most common forms are two species of viviparid, three species of hydrobiid (or pleuroceratid) gastropods and one species of corbiculid lamellibranch. The snail *Margarya melanoides* is economically important and externally resembles the thalassoid Tanganyikan Melaniidae. The most valuable fishes are *Cyprinus carpio*, *Carassius auratus* and *Schizothorax taliensis*.

6. A list of aquatic plants is given. Of these plants *Xystrobolus yunnanensis* is used as food while all the rest are used for fertilizing the fields about the lake.

7. Lake sediments show very low organic content with few remains of diatoms and invertebrates. Mechanical and chemical analyses of the cores indicate two probable dry periods when the sediment at the 56 and 100 cm. layers below the present bottom of the lake were deposited, with a zone formed during wetter period between them.

12. ACKNOWLEDGEMENTS

Our best thanks are due to Dr J. C. Bequaert of the Museum of Comparative Zoology for identifying the molluscs; to Dr E. D. Merrill of the Arnold Arboretum for identifying the higher plants; to Dr R. Patrick of the Academy of Natural Sciences of Philadelphia for similar work on diatoms; and to Dr F. Drouet of the Chicago Natural History Museum for determination of some of the Myxophyceae algae. Prof. G. E. Hutchinson of this Laboratory has given us his invaluable advice and encouraging help during the course of this study. We are very grateful to him.

REFERENCES

Annandale, N. & Prashad, B. (1919). Rec. Indian Mus. 16: 413–23.

Birge, E. A. & Juday, C. (1922). Bull. Wis. Geol. Nat. Hist. Surv. No. 64: 222 pp.

Birge, E. A. & Juday, C. (1934). Ecol. Monogr. 4: 440–74.

Boell, E. J. (1945). Trans. Conn. Acad. Arts Sci. 36: 429–41.

Brehm, V. (1924). Anz. Akad. Wiss. Wien, 7: 62–7; 13: 99–100.

Chang, H. & Chen, C. T. (1947). Science [Chinese] 29, No. 12: 13 (abstract).

Chaudhuri, B. L. (1911). Rec. Indian Mus. 6: 13–24.

Entz, G. (1906). 'Resultat der wissenschaftlichen. Erforschung des Balatonsees.' Wien. Bd. 2 (Anhang).

Heude, R. P. M. (1889). J. Conchyliol. (3) 29: 40–50; 225–9.

Hillebrand, W. F. & Lundell, G. E. F. (1929). 'Applied inorganic analysis.' New York.

Hsiao, S. C. (1946). J. Anim. Ecol. 15: 1–8.

Hsiao, S. C. (1948). Science, 107: 24–5.

Hutchinson, G. E. & Wollack, A. (1940). Amer. J. Sci. 238: 493–517.

Hutchinson, G. E., Wollack, A. & Setlow, J. K. (1943). Amer. J. Sci. 241: 533–42.

Jenkin, B. M. & Mortimer, C. H. (1938). Nature, Lond. 142: 834–5.

Jenkin, B. M., Mortimer, C. H. & Pennington, W. (1941). Nature, Lond. 147: 496–500.

Kieffer, J. J. (1911). Rec. Indian Mus. 6: 27–30.

Krumbein, W. C. (1939). 'Recent marine sediments.' Ed. Trask, Amer. Ass. Petroleum Geologists, Tulsa, Oklahoma: 558–91.

Krumbein, W. C. & Pettijohn, F. J. (1938). 'Manual of sedimentary petrography.' New York.

Lemmermann, E. (1903). ForschBer. Biol. Sta. Plön, 10: 116–71.

Lemmermann, E. (1908). Arch. Hydrobiol. Plankt. 3: 349–410.

Lu, T. H. (1939). Rep. Nat. Acad. Pekin, No. 20, Dec.: 1–16.

Pesta, O. (1930). Zool. Anz. 88: 132–8.

Pilsbry, H. A. & Bequaert, J. (1927). Bull. Amer. Mus. Nat. Hist. 53: 69–602.

Thiele, J. (1931–5). 'Handbuch der systematischen Weichtierkunde.' Jena. 2 vols.

West, G. S. (1916). 'Algae.' Vol. I: 433. Cambridge.

West, W. & West, G. S. (1909). Naturalist, 115–22, 134–41, 186–93, 260–7, 287–92, 323–31.

Yang (1930). Rep. Chinese Geol. Survey, 1930: 1.

THE DISTRIBUTION OF HARVESTMEN (PHALANGIDA) IN GREAT BRITAIN AND IRELAND, WITH NOTES ON THEIR NAMES, ENEMIES AND FOOD

By W. S. BRISTOWE

(With Six Figures and Twenty-one Maps in the Text)

1. INTRODUCTION

Harvestmen were known as 'shepherd spiders' four centuries ago and Dr T. Muffett (who completed the manuscript of his book in 1589) explained this by saying 'the English call it Shepherd either because it is pleased with the Company of Sheep or because Shepherds think those fields that are full of them to be good wholsome Sheep-pasture....'

Their association with agriculture is emphasized further both by Dr R. Hooke's use of the alternative names 'shepherd or carter spider' in 1658 in his *Micrographia* and by an old Essex superstition that it was unlucky for a reaper to kill one on purpose. This superstition arose from some belief that a harvestman helped farmerswith a scythe, rake and sickle which it was supposed to possess.

In France they are known as *faucheurs* (reapers) because, according to Littre's Dictionary, they give the appearance of reaping as they walk.

Only two species are at all conspicuous in our fields (*Phalangium opilio* and *Leiobunum rotundum*) and they are most noticeable in the harvest season when they reach maturity, so these two, and particularly the *Phalangium*, have been responsible for the name harvestman by which all species in the Order are now known. I can find no use of the name harvestmen before the early part of the nineteenth century. In view of a rhyme I shall be quoting later, I ought to mention that they have sometimes been called 'daddy-long-legs' and 'Harry-long-legs'. In 1746 B. Martin called them 'Carter or Father Long Legs'.

The name *Phalangium* is of eighteenth-century origin and the only explanation for this name that I can suggest is a remarkable one. In books up to the eighteenth century the name Phalangium had referred to poisonous spiders in southern Europe, such as *Latrodectus* which occasionally bit reapers in the fields. The 'Phalangium or phalanx spider' was so-called through likening it to a formidable soldier in a phalanx. These poisonous spiders did not extend into northern Europe, and the books, none of which described their appearance at all clearly, always emphasized their association with fields and harvests. Their absence in Sweden and their association with fields must, I think, have led to a confusion with harvestmen to which Linnaeus attached the genetic name *Phalangium* in 1758. Thus by 1758 the poisonous spiders had lost and the harvestmen had gained the name *Phalangium*.

In 1802 P. A. Latreille gave them the family name Phalangita which was altered to Phalangides by W. E. Leach in 1815 in order to conform with the termination of his other family names. Herbst had placed some species in a genus *Opilio* (shepherds) in 1798 and J. C. Sundevall introduced the family name Opiliones in 1833. E. Simon (1879), and many recent authors, followed Sundevall's name (elevated to the rank of Order) because of the confusion to which I have referred. Since this confusion occurred before the time of Linnaeus (1758), it ought to have no influence on post-Linnaean names and I recognize the earlier name, spelt in whatever may be the most suitable and correct manner—probably Phalangida—in preference to Opiliones. This, of course, is now an Order although it is not the kind of order which can be enforced!

2. ENEMIES

'The study of Harvestmen is a study of legs' wrote Savory in 1938, and they are indeed the feature which is bound to impress all observers. The ingenious Dr R. Hooke calculated in 1658 that 'an hundred and fifty times the strength of a man would not keep the body from falling on the breast' if his body were supported by legs of comparable length and similar design.

The ease with which harvestmen shed their legs must have contributed in some way to the cruel custom at Llanidloes (Montgomeryshire) of plucking them off one by one and then throwing the poor remnant to the ground whilst reciting the following lines:

Old Harry long legs
Cannot say his prayers.
Catch him by the right leg,
Catch him by the left leg
And throw him downstairs.

The legs give warning of approaching enemies or prey and harvestmen can stride out of serious harm's way with or without the loss of one of them. Should they come to grips with an aggressor, a fluid is exuded with a flavour distasteful to most other invertebrates. This protective measure does not seem to be fully

developed in young harvestmen and the remarks which follow do not apply to very young specimens which must be destroyed in considerable numbers by predaceous invertebrates.

Few spiders will sustain an attack on adult harvestmen. Usually they retreat after one bite and wipe their mouths on a leaf as I have recorded in experiments with nine British harvestmen in 1941 to which I could now add *Oligolophus tridens* C. L. K. Parasitic flies (Acroceridae, etc.), Pimpline ichneumons and hunting wasps (Pompilidae, Sphegidae) which prey on spiders avoid harvestmen. Predaceous flies, beetles and dragon-flies are not often to be found eating them. Harvestmen will, however, eat other harvestmen as I shall be mentioning later.

Protective measures are now realized to be more limited in effect than earlier naturalists sometimes supposed and in the case of harvestmen the exudation of a fluid does not provide protection against vertebrate animals. To start with such an unimportant 'enemy' as man, I have been told that *Phalangium opilio* has a nutty flavour to which an occasional schoolboy used not to be averse! Amongst vertebrates which pursue arthropods more seriously, I have records of fish, frogs, toads, lizards, birds and shrews eating harvestmen.

Fish will not often have the opportunity but I found a few harvestmen in the stomachs of brown trout (*Salmo trutta*) sent me from the Liffey by Miss W. E. Frost some years ago. These fish were caught just after a sudden substantial rise in the level of the river. *Phalangium opilio* has also been found in the stomach of a chub (*Squalius cephalus*).

In his examination of frog (*Rana temporaria*) and toad (*Bufo bufo*) stomachs, mostly in Cornwall between 1930 and 1935, Dr H. B. Cott has found the following nine species: *Anelasmocephalus cambridgei, Nemastoma lugubre, N. chrysomelas, Leiobunum rotundum, L. blackwalli, Oligolophus agrestis, Lacinius ephippiatus, Platybunus triangularis* and *Phalangium opilio*. Of these species *Nemastoma lugubre* was most frequently and most abundantly represented with *Phalangium opilio* an easy second.

Dr Cott has kindly supplied me with the following figures:

	No. of stomachs	Total food animals	Harvestmen
Rana temporaria	292	1500	17
Bufo bufo	350	9799	188

It is noteworthy that toads are grosser feeders than frogs, that they eat more harvestmen and that these represent a higher proportion of their diet. Although harvestmen were unevenly distributed, some stomachs containing several specimens and others none, the comparison can be made that on average there were six in every 100 frog stomachs and 54 in every 100 toad stomachs. In point of fact four of the frogs and 30 of the toads had eaten more than one harvestman and four particular toad stomachs contained no less than 13, 16, 18 and 21 harvestmen respectively.

British bird stomachs have also been found to contain harvestmen, but the most extensive data come from the United States. Mr C. Cottam of the Bureau of Biological Survey very kindly gave me figures which showed that an examination of 80,000 stomachs of birds representing all families in the U.S.A. yielded 9966 spiders, 795 harvestmen and 189 pseudoscorpions. The most constant consumers of harvestmen appeared to be *Colinus virginianus, Coccyzus americanus* and *C. erythropthalmus*.

3. FOOD

It has usually been the fate of harvestmen to be noticed in passing by arachnologists like myself whose principal interest lay in spiders. Only isolated prey records have been recorded leaving doubts as to whether they were chiefly predators or scavengers and whether they were partially vegetarians. Extensive night work and experiments on captive specimens are needed to supply the answer; but even my own modest contribution to the subject provides more than a combination of all published records. It also exposes the fallacy of the statement made by Savory (1938) that 'unlike spiders, they are not cannibals'. It shows: (1) that harvestmen attack other harvestmen, living snails, worms, millipedes, woodlice, spiders, leaf-hoppers, earwigs, flies and other small invertebrates as opportunity offers; (2) that they act as scavengers of dead animal material including bird-droppings, millipedes, centipedes, ants, spiders, flies, beetles, etc.; and (3) that they will occasionally browse the gills of the chanterelle* and possibly other fungi, and chew pellets of miscellaneous vegetable matter which they have carried to a suitable feeding ground such as the top of a leaf. I have also seen one scouring the inside of a nutty seed of some unidentified plant.

A light shone on plantain and other broad leaves fringing my garden drive in Sussex 2 hr. after dark in September and October shows numerous *Oligolophus tridens* of which about half are eating something. The food has often been reduced to an unidentifiable pulpy pellet.

My results, by torchlight unless otherwise mentioned, are listed below:

(1) **Leiobunum rotundum.** Prey: a mosquito (*Culex*); a harvestman (*Oligolophus tridens* C. L. K.); a woodlouse (*Philoscia*); a beetle larva.

(2) **Leiobunum blackwalli.** Prey: bird-dropping; a fly (*Lonchaea chorea* (Fabr.)); leaf-hoppers

* I saw several harvestmen, too young to identify, doing this in Argyllshire in 1947.

(Jassidae) twice; a harvestman (*Oligolophus tridens*); a small earthworm; a millipede.

(3) **Mitopus morio.** Prey: harvestmen (*Oligolophus agrestis*, *O. tridens*, *Mitopus morio*); an earwig; an ant, *Myrmica*; a leaf-hopper (Cercopidae); a small earthworm. In captivity, a spider (*Drapetisca socialis* Sund.).

(4) **Oligolophus tridens.** Prey: a pellet of vegetable matter (twice); the inside of a nutty seed; bird-dropping; a small snail (*Trichia hispida* (L.)); millipedes (twice); a harvestman (*Mitopus morio*); spiders (*Oxyptila trux* Bl. (twice)); homopterous bugs (a jassid and a psyllid); a chrysomelid beetle; a small beetle; a mite; four woodlice (*Philoscia*); a small muscid fly; a lepidopterous larva. In captivity: caught a fly (*Lonchaea chorea* (Fabr.)) and ate a dead *Musca domestica* L.

(This species has been captured in copula at 9.30 p.m. as late as 23 October.)

(5) **Oligolophus agrestis.** Prey: two sharing a bird-dropping; a springtail (Collembola); a small adult snail (*Trichia striolata* (Pfeiffer); a woodlouse (*Philoscia*); a stratiomyid larva (*Geosargus*); a small green lepidopterous larva. In captivity ate a spider (*Drapetisca socialis* Sund.).

(6) **Megabunus diadema.** Fab. Prey: in daytime, eating a chironomid fly.

(7) **Phalangium opilio.** Linn. Prey: in daytime, eating a spider (*Theridion ovatum* Clerck). At night, a harvestman (*Oligolophus tridens*), an aphid and a noctuid larva. In captivity caught a fly (*Stomoxys calcitrans* (L.)).

Sometimes the victims appeared to have been found dead (to judge by small fragments of earth attached to them) but more often they looked fresh. A millipede, two earthworms and two snails were still capable of movement.

I am indebted to Mr A. W. Stelfox for identifying one of the snails, *Trichia striolata* (Pf.), which I found in Eire. He himself once found *Phalangium opilio* L. with a *Helix* (*Cochlicella*) *acuta* (Müller).

The other snail, *Trichia hispida* (L.), was identified by Mr A. E. Ellis and the stratiomyid larva by Dr O. W. Richards.

4. THE BRITISH SPECIES

The Rev. O. Pickard-Cambridge recognized 24 species in his *Monograph of The British Phalangidea or Harvest-men* in 1890. He subsequently added *Oligolophus hanseni* Kraep. to the list in 1897. In 1935 I added *Nelima silvatica* Sim. to the list. Despite these additions there are now believed to be only 21 species in Britain because some of the species in O. Pickard-Cambridge's list are recognized to have been varieties or immature forms of other species.

Recent lists published by Miss V. Todd and by T. H. Savory (both in 1948) differed in one important respect. Miss Todd reconstituted *Opilio saxatilis* C.L.K. as a species distinct from *O. parietinus* Deg. T. H. Savory followed most recent authors in regarding the former as a synonym of the latter in accordance with C. F. Roewer's conclusion (1923). In the hope of removing the doubt which so clearly existed I invited Miss Todd and Mr Savory to dissect both species and to examine the genitalia of the males and females whilst I did likewise. Our independent conclusions were identical: (1) *O. saxatilis* is certainly not an immature form of *O. parietinus*, (2) the male penis is easily distinguishable and there may be constant though very small differences in the female's ovipositor, and (3) the two forms should be regarded as distinct species. The external appearance of the two species is so different as to make identification easy without the need for dissection now dissection has confirmed the belief of writers before 1923 that the species are distinct. Nevertheless, it would be interesting to seek further confirmation by placing together living males of *O. saxatilis* with females of *O. parietinus* and vice versa.

The three distinguishing features in the male penis are illustrated in Figs. 1–4:

(*a*) Though subject to some variation in individual specimens examined, the glans penis of *O. parietinus* is relatively longer and of somewhat different shape (see Figs. 3 and 4).

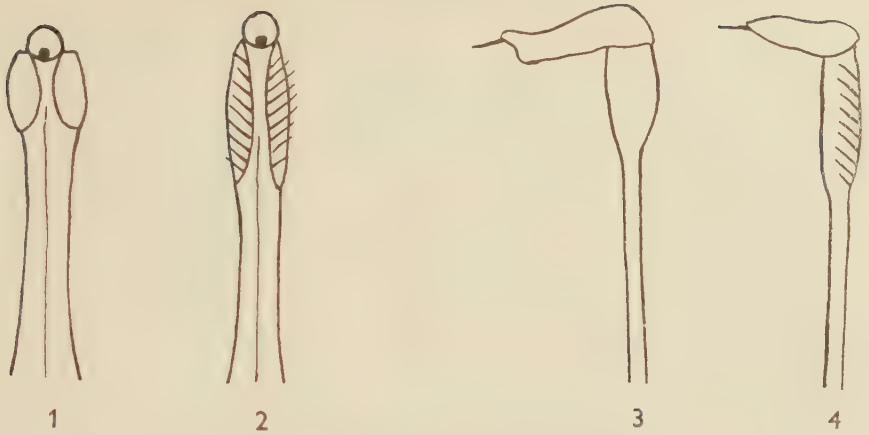
(*b*) The penis tube has two plates at its extremity. In *O. parietinus* these are shorter and the extremity of the tube has a more bulbous appearance (see Figs. 1 and 2).

(*c*) These plates bear a series of bristles in *O. saxatilis* which are absent in *O. parietinus* (see Figs. 1 and 2).

Such minor differences as occur in the ovipositor could be due to the difference in size of *O. parietinus* and *O. saxatilis* (see Figs. 5 and 6 prepared from sketches by Miss V. Todd).

Since writing the above I have learned that J. H. P. Sankey and D. G. Brown had previously reached the same conclusions after examining the genitalia and that the former had submitted a paper to the Zoological Society for publication in the Proceedings. Our work happily confirms J. H. P. Sankey's investigations.

T. H. Savory (1948) also followed C. F. Roewer (1923) in placing *meadei* Camb. in the genus *Odiellus* but he now agrees with me that Miss Todd (1948) is correct in transferring it back to *Oligolophus*. Since this species is confined to Britain, C. F. Roewer may have lacked the opportunity to examine it.



Figs. 1, 3. Penis of *O. parietinus* Deb. Dorsal and lateral views respectively.
Figs. 2, 4. Penis of *O. saxatilis* C.L.K. Dorsal and lateral views respectively.

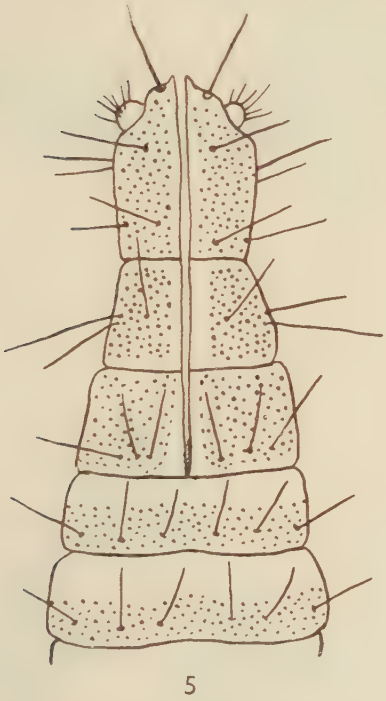


Fig. 5. Ovipositor of *O. parietinus* Deb.

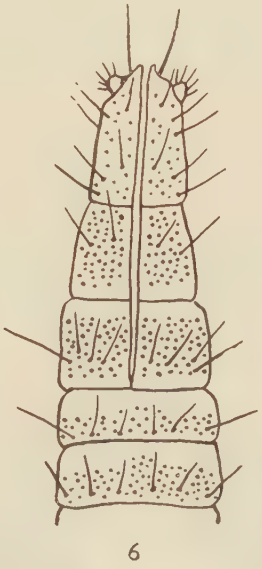
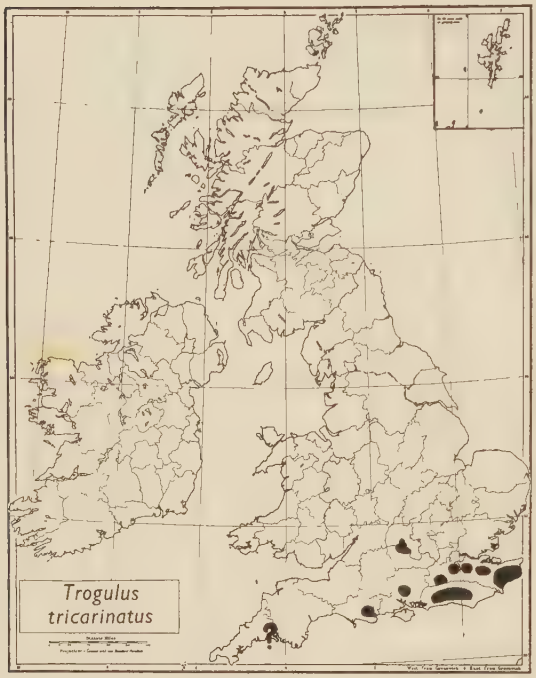


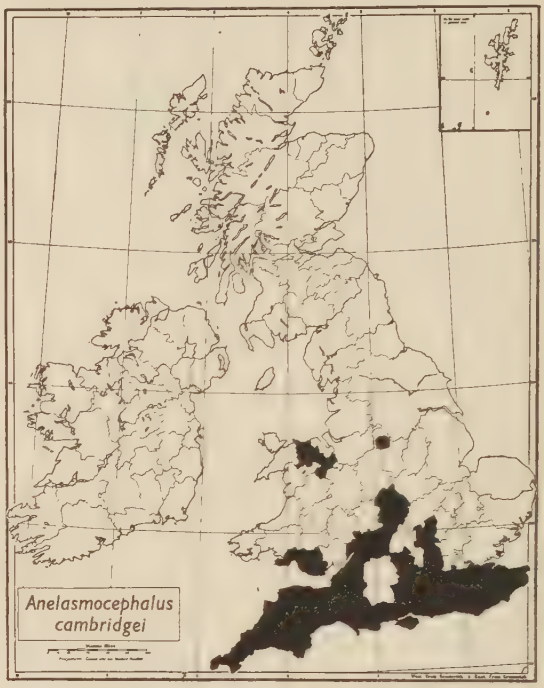
Fig. 6. Ovipositor of *O. saxatilis* C.L.K.

5. DISTRIBUTION

The chief contribution I can make is to the knowledge of the distribution of harvestmen. Wherever I have searched for spiders, harvestmen have also been collected. My collections have been made in 69 counties. These include all the counties of England except Worcestershire, Yorkshire, Westmorland, Cumberland and Durham, 9 in Wales (all except Glamorganshire, Denbighshire and Anglesey), 13 in Scotland and 11 in Ireland.

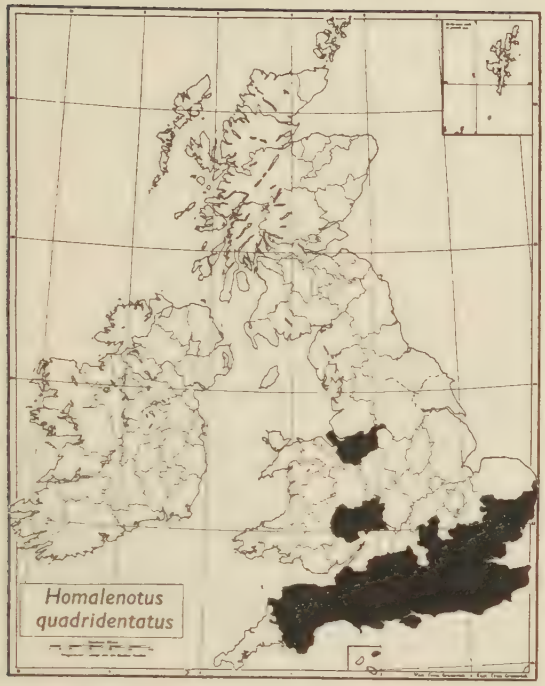
My hunting grounds have included many islands and have ranged from the Channel Islands and Scilly Islands in the south, to the Skelligs and Blaskets in the west and to the Outer Hebrides, Orkneys and Shetlands in the north. Harvestmen have been collected from sandhills and the seashore to altitudes above 3000 ft. in Wales, Scotland and Ireland.


Trogulus
tricarinatus


Anelasmocephalus
cambridgei

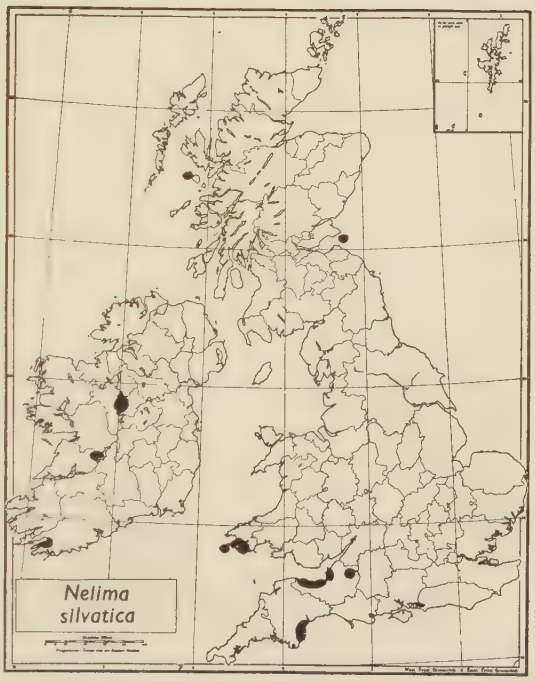
Nemastoma
lugubre

Nemastoma
chrysomelas

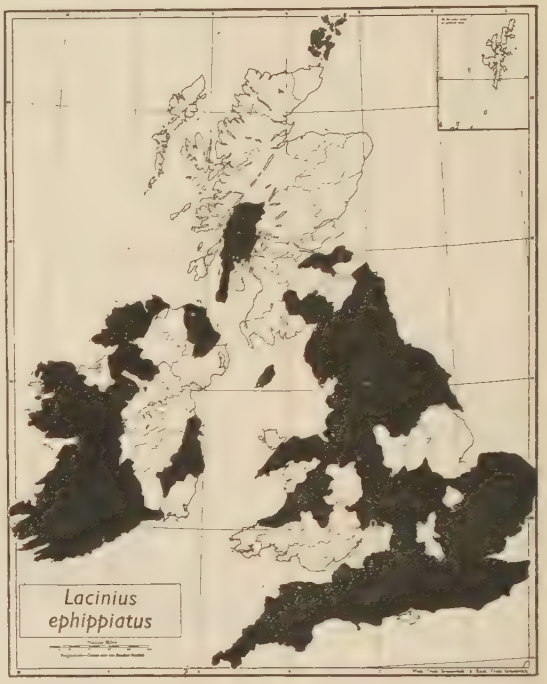

Homalenotus
quadridentatus

Leiobunum
rotundum

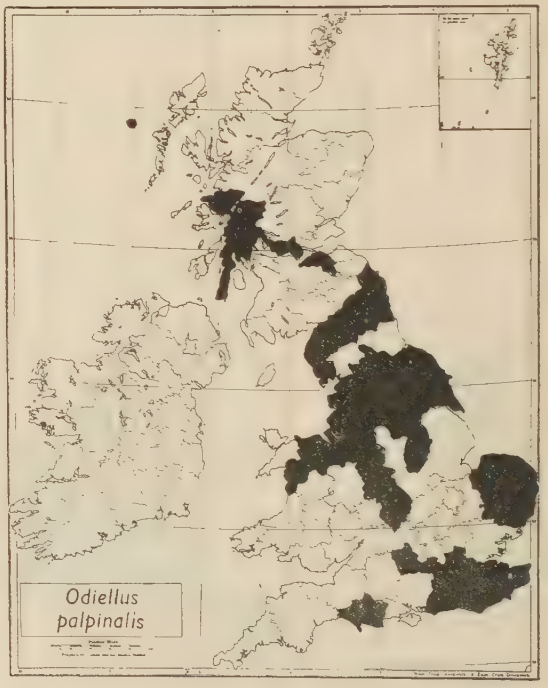
Leiobunum
blackwalli


Nelima
silvatica

Mitopus
morio


Lacinius
ephippiatus

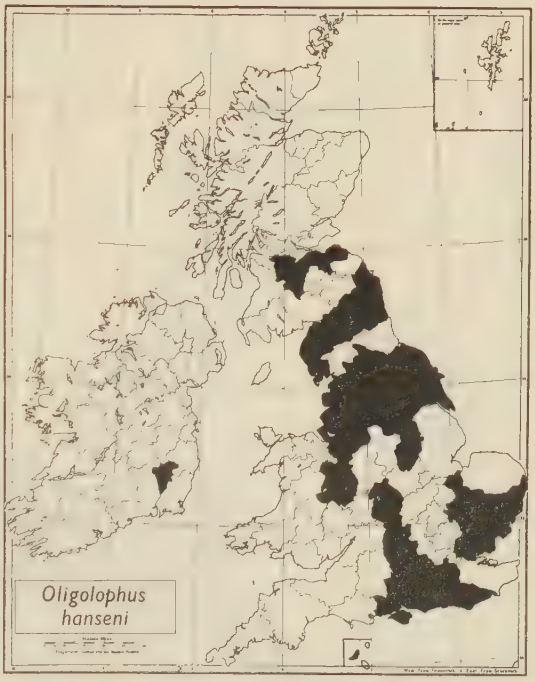
Odiellus
spinosus


Odiellus
palpinalis

Oligolophus
meadei

Oligolophus
tridens

Oligolophus
agrestis


Oligolophus
hanseni

Platybunus
triangularis

Megabunus
diadema

Phalangium
opilio

Opilio
parietinus

With several enthusiasts now taking a special interest in harvestmen, the time seemed to have arrived to publish this considerable accumulation of records and to add the published records of other workers in order to show the present state of our knowledge.

The principal contributors are easier to list than the mass of papers, usually dealing with spiders, from which short lists have been extracted after extensive combing of the literature. I owe most to the records of D. Pack Beresford as the principal recorder of Irish species because I have been able to add comparatively few myself. W. Evans was the most extensive collector in Scotland. O. Pickard-Cambridge, W. Falconer, A. R. Jackson and T. H. Savory have contributed most to the English and Welsh lists. Apart from these authors there have been a host of lesser contributors including F. O. Pickard-Cambridge, J. E. Hull, G. H. Carpenter, C. Warburton, R. Butterfield, R. H. Meade, A. E. Ellis, J. H. Bloom, E. D. Marquand, T. Stainforth, H. Britten, J. W. Carr and L. A. Carr.

T. H. Savory's unpublished additions, which he has kindly allowed me to use, are as follows: (1) *Platybunus triangularis* from Herefordshire, Bedfordshire and Cardiganshire; (2) *Leiobunum rotundum* from Herefordshire; (3) *Oligolophus tridens* from Devon, Kent, Westmorland and Sutherland; (4) *O. agrestis* from Bedfordshire; (5) *Mitopus morio* from Bedfordshire (and Tiree); (6) *Lacinius ephippiatus* from Bedfordshire; (7) *Opilio parietinus* from Bedfordshire and Cardiganshire; (8) *Nemastoma chrysomelas* from Worcestershire; (9) *Phalangium opilio* from Cardiganshire, Westmorland (and Tiree); (10) *Megabunus diadema* from Sutherland.

I am indebted to Miss V. Todd for six records new to me from Berkshire: *Trogulus tricarinatus*, *Anelasmocephalus cambridgei*, *Odiellus palpinalis*, *Oligolophus meadei*, *O. hanseni* and *Platybunus triangularis*.

From a list of seven species from Westmorland kindly supplied to me by Mr N. A. Locket, *Platybunus triangularis* and *Opilio parietinus* were new to my records.

Dr N. Richter has been kind enough to collect seven species for me from Elgin: *Nemastoma lugubre*, *Mitopus morio*, *Oligolophus tridens*, *O. agrestis*, *Platybunus triangularis*, *Megabunus diadema* and *Phalangium opilio*. G. W. Whatmough has done likewise in Lincolnshire and his collection of eight species has added *Oligolophus tridens* to the list for that county.

Mr J. H. P. Sankey has kindly allowed me to include his new records: (1) *Trogulus tricarinatus* in Kent, Sussex, Surrey and Hampshire; and also (2) *Nemastoma chrysomelas* from Essex, Suffolk and Pembrokeshire; (3) *Homalenotus quadridentatus* from Suffolk; (4) *Leiobunum rotundum* from Haddingtonshire; (5) *L. blackwalli* from Essex, Denbighshire and Flintshire; (6) *Nelima silvatica* from three localities in Pembrokeshire; (7) *Mitopus morio* from Skokholm (Pembrokeshire); (8) *Odiellus spinosus* from Norfolk and Flintshire; (9) *O. palpinalis* from Suffolk and Flintshire; (10) *Oligolophus meadei* from Suffolk and Surrey; (11) *O. tridens* from Gloucestershire and Denbighshire; (12) *O. agrestis* from Gateholm; (13) *O. hanseni* from Essex and Kent; (14, 15) *Platybunus triangularis* and *Megabunus diadema* from Essex; (16) *Phalangium opilio* from Gateholm and Flintshire; (17) *Opilio parietinus* from Gloucestershire and Flintshire; and (18) *O. saxatilis* from Wilts and Derby.

Mr D. G. Brown has kindly supplied me with the following new records: *Trogulus* from various localities in Kent and Surrey; *Nemastoma lugubre* from Canna; *Leiobunum blackwalli* from Bedfordshire and Warwickshire; *Nelima* from Somerset and Canna; *Odiellus spinosus* from Somerset; *O. palpinalis* from Kent; *Oligolophus tridens* from Somerset and Cambridgeshire; *O. agrestis* from Canna; *Phalangium opilio* from Canna; and *Opilio parietinus* from Warwickshire.

Distribution maps illustrate the present state of our knowledge, which is summarized in the notes which follow. The names of islands, mountains or counties printed in italics in the notes represent the records of my own collecting. In a few cases they are records of specimens sent to me for identification by correspondents, e.g. Elgin, Bardsey and the Isle of May.

My own collecting has provided 561 of the County records.

1. **Trogulus tricarinatus** Linn.

A southern species which favours chalk soils in beechwoods, etc. In recent years it has been found by Miss Todd in Berkshire, by D. G. Brown in several localities in Kent and at Ewhurst in Surrey, and by J. H. P. Sankey at several places in Sussex and Kent, and at Addington (Surrey) and Winchester (Hampshire).

Some doubt may be felt as to the reliability of a record from Cornwall because it was based on an immature specimen away from chalk (O. Pickard-Cambridge, 1907). A record from Deepdale, Derbyshire, I have decided to omit. When A. R. Jackson found the specimen in 1899 on which the record depends he had not himself started to study harvestmen, and F. O. Pickard-Cambridge, who identified it, never made a special study of them. It was an immature specimen and in 1907 Jackson wrote with some caution: 'Probably it was referable to this species, but the specimen is now lost.' In later years Jackson returned to Deepdale on several occasions but only succeeded in finding several specimens of *Anelasmocephalus cambridgei*. Having heard in 1942 that H. Britten had been more successful in refinding *Trogulus* in Derbyshire at Fernilea, he examined these specimens and found they too were *Anelasmocephalus cambridgei*. The conclusion I reach is that *Trogulus* has not been found in Derbyshire; nor do I expect it to be found so far north.

England: Surrey (Ewhurst, Addington); Sussex (Poynings, Arundel, Ashurst); Kent (Cudham, Wye, Chilham, Molash, Godmersham, Challock, Crundale, Boxley, Hougham, Alkham, Folkestone, Walder-shore); ? Cornwall (Rame Head); Dorset (Bloxworth); Berkshire (Wytham Wood); Hampshire (Winchester).

2. **Anelasmocephalus cambridgei** Westw.

Mainly a southern species restricted to limestone soils.

England: Cornwall, Devon, Dorset, Hampshire, Isle of Wight, *Somerset*, *Sussex*, *Surrey*, Kent, Berkshire, Buckinghamshire, Gloucestershire, Warwickshire, Derbyshire.

Wales: Glamorganshire, Denbighshire.

3. **Nemastoma lugubre** Müll.

A ground-living species which is likely to be found in every county. I myself have collected it in 62 counties. Islands include *Guernsey*, *Jersey*, *Isle of Wight*, *Skomer*, *Ramsey*, *Bardsey*, Anglesey, Isle of Man, *Arran*, *Jura*, *Rum*, *Eigg*, Canna, *Skye*, *Priest Island*, *Summer Island*, *Shiant Island*, *Lewis*, St Kilda, *Orkneys*, *Blaskets*, Clare Island, Tory Island, Lambay.

On mountains it extends up to 3500 ft. Snowdon, *Halival*, *Suilvin*, Schiehallion, Ben Nevis, *Carrantual*, and *Brandon*.

England: All counties.

Wales: All counties.

Scotland: All counties except Roxburghshire, Wigtown, Dumbartonshire, Selkirkshire, and Peeblesshire.

Ireland: All counties except Wexford, Leix, Wicklow, Kildare, Meath, Longford, Monaghan, Tyrone.

4. **Nemastoma chrysomelas** Herm.

This marsh and hill species appears to be scarce in Ireland. Not yet found in the extreme north of Scotland.

Found at or near the summit of several of our higher mountains including Snowdon, *Cader Idris*, Glyder Fawr, *Brecon Beacons*, and Ben Nevis.

Recorded from the Cheddar Caves 50 ft. from the entrance.

England: *Cornwall*, *Devon*, *Dorset*, *Somerset*, *Wiltshire*, *Hampshire*, Isle of Wight, *Sussex*, *Surrey*, *Kent*, Essex, *Gloucestershire*, Oxfordshire, *Buckinghamshire*, *Berkshire*, *Hertfordshire*, *Northamptonshire*, Middlesex, Suffolk, Norfolk, Herefordshire, Worcestershire, Staffordshire, *Derbyshire*, Nottinghamshire, *Cheshire*, *Lancashire*, Isle of Man, Yorkshire, Durham, Cumberland, Westmorland, *Northumberland*.

Wales: *Brecon*, *Merioneth*, *Caernarvonshire*, Pembrokeshire.

Scotland: Berwickshire, Stirlingshire, Lanarkshire, Perthshire, *Argyllshire*, Haddingtonshire, Edinburgh, *Inverness-shire*.

Ireland: Carlow.

5. **Homalenotus quadridentatus** Cuv.

(*Sclerosoma romanum* L. Koch—O. P.-Cambridge)

Mainly a southern species on chalk and limestone soils.

England: Alderney, Devon, Dorset, Somerset, Wiltshire, Hampshire, *Isle of Wight*, *Sussex*, *Surrey*, *Kent*, Middlesex, *Essex*, *Hertfordshire*, *Buckinghamshire*, *Berkshire*, Suffolk, Herefordshire, Worcestershire, Cheshire.

6. **Leiobunum rotundum** Latr.

Likely to be found in every county with the possible exception of those in the extreme north of Scotland.

I have found it in 59 counties in fields, woods and marshland, amongst bracken, heather, grass, brambles, etc., and on tree trunks as the season progresses to September.

The islands it inhabits include *Guernsey*, *Scilly*, *Lundy*, *Isle of Wight*, Isle of Man, Anglesey and *Arran*.

England: All counties.

Wales: All counties *except* Glamorganshire.

Scotland: Berwickshire, *Edinburgh*, *Linlithgowshire*, *Bute*, *Lanarkshire*, Renfrewshire, *Ayrshire*, *Argyllshire*, Fifeshire, Haddingtonshire.

Ireland: *Kerry*, *Cork*, *Limerick*, *Tipperary*, *Offaly*, Dublin, *Clare*, *Leitrim*, Carlow, Louth, *Galway*, *West Meath*, *Longford*, Mayo, Sligo, *Roscommon*, Cavan, Londonderry, Antrim, Fermanagh.

7. **Leiobunum blackwalli** Meade.

Appears to be unusual in Scotland and the northern counties of Ireland. It frequents woods, grassland, marsh and bracken. I have found it in London gardens at Holland Park.

Islands include *Guernsey*, *Jersey*, *Isle of Wight*, *Scilly*, *Lundy*, *Skokholm*, *Valentia*.

England: All counties *except* Huntingdonshire, Shropshire, Leicestershire, Northumberland.

Wales: *Pembrokeshire*, *Montgomeryshire*, Denbighshire, *Merioneth*, Flintshire, *Caernarvonshire*.

Scotland: Edinburgh.

Ireland: *Kerry*, *Cork*, Waterford, Carlow, *Clare*, Dublin, *Leitrim*, Meath, *West Meath*, Galway, Louth, Mayo, Down.

8. **Nelima silvatica** Sim.

Having discovered this species in Britain for the first time on Skokholm in 1934, I was sent a specimen, together with some spiders, from the Isle of May a month later by the owner of Skokholm (Mr R. M. Lockley). He was unaware of the appearance of *Nelima* and was positive no confusion had occurred as he had collected no 'Spiders' on Skokholm. Since then I have received specimens from Canna off the West Coast so I now have no lingering doubts about the Isle of May record.

In 1938 Dr A. R. Jackson and I found specimens near the seashore at Minehead. In 1948 I got a specimen near the shore at Bantry Bay, Cork, and later at three places inland in Clare, Longford and Roscommon beside Lough Dearg and near the Shannon banks.

Mr C. Elton and Mr A. E. Ellis have found this species on the coast in Pembrokeshire and Devon respectively. Mr J. H. P. Sankey has sent me specimens from the Pembrokeshire coast and Mr D. G. Brown from Somerset and Canna.

This suggests that *Nelima*, though overlooked for so long, will be discovered in many parts of Britain and perhaps in most coastal districts.

England: *Somerset* (Minehead, Berrow, Monkton Combe), Devon (Babbacombe).

Wales: *Pembrokeshire* (Skokholm, Gateholm, Dale, Littlehaven, Marloes).

Scotland: *Isle of May* and Canna.

Ireland: *Cork* (Bantry Bay), *Clare* (Mountshannon), *Longford* and *Roscommon* (near Lanesborough).

9. **Mitopus morio** Fabr.

(*Oligolophus alpinus*, *O. cinerascens*)

Can be expected in every county. It inhabits woods, marshland, fields and mountains. The mountain form, *Mitopus morio alpinus*, extends to the summit or near the summit of many of the higher mountains including Snaefell, High Street, *Brecon Beacons*, *Aran Fawddy*, Moel Siabod, Carnedd Davydd, Snowdon, Ben Lomond, *Merrick*, *Ben Cruachan*, *Ronas Hill* (Shetlands), Croaghpatrick, Mangerton, Mount Leinster, *Carrantual* and *Brandon*.

It extends northwards to the Faeroes and is the only species to inhabit Iceland and Greenland. On our own islands it inhabits the *Isle of Wight*, Isle of Man, Skokholm, Anglesey, *Rum*, *Skye*, Tiree, *Priest Island*, *Arran*, *Shiant Island*, St Kilda, *Orkneys*, *Shetlands*, Dursey, Inishmore, Lambay, Clare Island, and Caher Island.

England: All counties *except* Herefordshire, Huntingdonshire, Monmouthshire.

Wales: All counties *except* Radnorshire.

Scotland: All counties *except* Nairnshire, Kincardineshire, Angus, Peeblesshire, Selkirkshire, Roxburghshire, Wigtown.

Ireland: All counties *except* Waterford, Kilkenny, Wexford, Kildare, Monaghan.

10. **Lacinius ephippiatus** C.L.K.

A wide distribution in woods, fields and marshland from the south coast to the Orkneys.

The Isle of Man, Orkneys and Clare Island are the only islands on which it has been noticed.

England: *Cornwall*, *Devon*, *Somerset*, Dorset, Wiltshire, *Hampshire*, *Sussex*, *Surrey*, *Kent*, *Middlesex*, Essex, *Hertfordshire*, *Berkshire*, Oxfordshire, Bedfordshire, Norfolk, *Suffolk*, Cambridgeshire, Leicestershire, Warwickshire, *Rutland*, *Northamptonshire*, Worcestershire, Staffordshire, *Cheshire*, Lancashire, Yorkshire, Westmorland, Cumberland, Durham, *Northumberland*.

Wales: Cardiganshire, *Radnorshire*, Flintshire, Denbighshire, *Caernarvonshire*, *Montgomeryshire*.

Scotland: Dumfriesshire, Edinburgh, Haddingtonshire, *Argyllshire*.

Ireland: *Kerry*, *Cork*, Waterford, Carlow, *Clare*, Wicklow, Dublin, *Tipperary*, *Limerick*, *Roscommon*, *Galway*, *Leitrim*, Mayo, Fermanagh, Donegal, Antrim.

11. **Odiellus spinosus** Bosc.

Found especially in gardens (including *Hampstead*) but not one of our commoner species and apparently confined to the south and midlands. A record from Yorkshire was subsequently corrected to *O. tridens* by W. Falconer.

England: *Cornwall*, *Devon*, Somerset, Dorset, Wiltshire, Gloucestershire, Hampshire, *Sussex*, *Surrey*, *Kent*, *Middlesex*, *Hertfordshire*, Oxfordshire, *Berkshire*, Essex, *Cambridgeshire*, Norfolk, *Suffolk*, *Rutland*, *Northamptonshire*, Lincolnshire, Warwickshire, Leicestershire, Worcestershire.

Wales: Flintshire.

12. **Odiellus palpinalis** Herbst.

Not yet recorded from Ireland or northern Scotland (except St Kilda), this species inhabits marshes, woods, and fields.

England: Dorset, *Sussex*, *Surrey*, Kent, Middlesex, Berkshire, Suffolk, Norfolk, Warwickshire, Cheshire, Lancashire, Staffordshire, Nottinghamshire, Yorkshire, Cumberland, Northumberland.

Wales: *Merioneth*, Denbighshire, Flintshire.

Scotland: Edinburgh, *Argyllshire*, Stirlingshire, St Kilda.

13. **Oligolophus meadei** Camb.

This species, transferred back to this genus from *Odiellus* as previously explained, is the only one not yet recorded on the Continent. It has been reported from Guernsey but nowhere else outside England.

England: *Cornwall*, Dorset, *Sussex*, Surrey, *Kent*, Berkshire, Suffolk, Staffordshire, Cheshire, Lancashire, Cumberland.

14. **Oligolophus tridens** C.L.K.

Likely to be found in every county in woods, marshy ground, fields and gardens.

Known from the following islands: Isle of Wight, Isle of Man, *South Rona*, *Orkneys*, *Shetlands*, Lambay.

England: *Cornwall*, *Devon*, Somerset, *Dorset*, *Hampshire*, *Sussex*, *Surrey*, *Kent*, *Middlesex*, *Essex*, *Buckinghamshire*, *Berkshire*, *Hertfordshire*, Gloucestershire, Cambridgeshire, *Oxfordshire*, *Suffolk*, Norfolk, Worcestershire, Nottinghamshire, *Warwickshire*, *Northamptonshire*, *Leicestershire*, *Rutland*, *Bedfordshire*, *Cheshire*, *Lancashire*, Staffordshire, Yorkshire, *Derbyshire*, *Lincolnshire*, *Northumberland*, Cumberland, Westmorland.

Wales: Glamorganshire, *Pembrokeshire*, *Cardiganshire*, *Montgomeryshire*, Flintshire, *Merioneth*, Denbighshire.

Scotland: *Kirkcudbrightshire*, Berwickshire, *Edinburgh*, Haddingtonshire, Linlithgowshire, Renfrewshire, Lanarkshire, Stirlingshire, *Ayrshire*, *Elginshire*, *Argyllshire*, *Caithness*, Sutherland.

Ireland: *Cork*, *Kerry*, Kilkenny, Wexford, Carlow, Wicklow, *Tipperary*, *Galway*, Dublin, *Offaly*, *West Meath*, *Leitrim*, Meath, Louth, *Roscommon*, *Longford*, *Clare*, Sligo, Fermanagh, Armagh, Down, Donegal, Londonderry, Antrim.

15. **Oligolophus agrestis** Meade.

Likely to be found in every county and I have collected it in 52 myself. Inhabits marshland, fields, woods and gardens. It has been found both in a hedgehog's and a carrion crow's nest. Though not usually an inhabitant of mountains, it has been found at the summit of Snaefell (2030 ft.).

Island records include *Guernsey*, *Isle of Wight*, *Skokholm*, Gateholm, Isle of Man, *Arran*, *Isle of May*, Bass Rock, *South Rona*, Canna.

England: All counties.

Wales: All counties *except* Radnorshire and Glamorganshire.

Scotland: *Kirkcudbrightshire*, *Bute*, Banffshire, Berwickshire, *Ayrshire*, Stirlingshire, *Edinburgh*, Lanarkshire, Haddingtonshire, Linlithgowshire, Renfrewshire, Dumfriesshire, Dumbartonshire, *Elginshire*, Fifeshire, *Argyllshire*, *Sutherland*.

Ireland: All counties *except* Wexford, Leix, Kildare, Louth, Cavan, Sligo.

16. **Oligolophus hanseni** Kraep.

Associated with trees and shrubs from the branches of which it may be beaten. Apparently scarce in Ireland and Scotland, and not yet recorded from Wales. Reported from Guernsey and the Isle of Wight.

England: Hampshire, *Sussex*, *Surrey*, Kent, Berkshire, Oxfordshire, *Suffolk*, Essex, *Cambridgeshire*, Warwickshire, Shropshire, Nottinghamshire, *Cheshire*, Lancashire, Yorkshire, Cumberland, Northumberland.

Scotland: Edinburgh, Haddingtonshire, Lanarkshire.

Ireland: Carlow.

17. **Platybunus triangularis** Herbst.

(*P. corniger*)

This species may live in every county and I myself have found it in thirty.

Its known distribution includes the Isle of Wight, *Skomer*, *Ramsey*, *Bardsey*, Anglesey, *Arran* and *Scarif*.

In 1937 I found it commonly in a garden in *London* at Holland Park.

England: All counties *except* Buckinghamshire, Leicestershire, Monmouthshire, Rutland.

Wales: Glamorganshire, *Pembrokeshire*, Cardiganshire, *Merioneth*, Denbighshire, Flintshire, *Caernarvonshire*.

Scotland: Ayrshire, Bute, Stirlingshire, *Renfrewshire*, Lanarkshire, Edinburgh, Haddingtonshire, Linlithgowshire, Perthshire, *Argyllshire*, Inverness-shire, *Elginshire*.

Ireland: *Kerry*, *Cork*, Carlow, Wicklow, Galway, Kildare, Dublin, Roscommon, Louth, Mayo, Leitrim, Fermanagh, Tyrone, Armagh, Donegal, Londonderry.

18. **Megabunus diadema** Fabr.

(*M. insignis*)

This species lives mostly on tree-trunks and on rocks. Sometimes it extends to altitudes of 2000 ft. on mountains (*Carrantual*, *Brandon*).

It is likely to be found in every county.

On islands it has been found in the *Isle of Wight*, *Skomer*, Isle of Man, Clare Island, Aran (Donegal), *Lewis* and the *Orkneys*.

England: All counties *except* Cambridgeshire, Northamptonshire, Rutland, Lincolnshire, Herefordshire, Monmouthshire, Westmorland.

Wales: *Pembrokeshire*, *Merioneth*, *Caernarvonshire*, *Montgomeryshire*.

Scotland: Ayrshire, Stirlingshire, Fifeshire, Linlithgowshire, Edinburgh, Haddingtonshire, Lanarkshire, *Renfrewshire*, *Argyllshire*, Perthshire, *Elginshire*, *Inverness-shire*, Sutherland.

Ireland: *Kerry*, *Cork*, Limerick, Clare, Carlow, Wicklow, Offaly, Dublin, Galway, Roscommon, Louth, Mayo, Sligo, Leitrim, Monaghan, Fermanagh, Armagh, Down, Antrim, Donegal.

19. **Phalangium opilio** Linn.

Likely to be found in every county. Occurs in fields, gardens, heaths, sandhills, etc., and on many islands: *Jersey*, *Guernsey*, Alderney, *Isle of Wight*, *Scilly*, Gateholm, *Skokholm*, *Bardsey*, Anglesey, Isle of Man, *Arran*, May Island, Tiree, *Rum*, Canna, *Kerrera*, *Orkneys*, *Shetlands*, *Scarif*, *Blaskets*, *Seven Hogs*, Inishmore, Clare Island, Tory Island, Lambay, Inishmacdara.

England: All counties.

Wales: All counties.

Scotland: All counties *except* Wigtown, Roxburghshire, Selkirkshire, Peeblesshire, Kincardineshire, Banffshire, Nairnshire, Dumbartonshire, Clackmannanshire, Kinross-shire.

Ireland: All counties *except* Waterford, Kildare, Meath, Cavan, Monaghan, Armagh.

20. **Opilio parietinus** De Geer.

Likely to be found in all counties except in northern Ireland and Scotland. Often common in gardens and on walls. In 1935 I found it in a yard at the Angel, *London*.

Island records comprise Alderney and the *Isle of Wight*.

England: All counties *except* Monmouthshire, Huntingdonshire, Rutland, Leicestershire, Durham.

Wales: Denbighshire, *Caernarvonshire*, Cardiganshire, Flintshire.

Scotland: Ayrshire, Edinburgh, Lanarkshire, Fifeshire.

Ireland: Carlow, Wicklow, *West Meath*, *Roscommon*, *Leitrim*, Mayo, Sligo.

21. **Opilio saxatilis** C.L.K.

Most authors have regarded this as a synonym of *O. parietinus* for 25 years and its known distribution is, in consequence, less than would otherwise be the case. It is likely to be found in all counties except in the north of Ireland and Scotland.

Like the last species it is found in gardens, but it is associated more with downs, heaths, and sand dunes.

It is found in *Guernsey* and the Isle of Wight.

England: *Cornwall*, *Devon*, *Dorset*, Wiltshire, *Hampshire*, *Sussex*, *Surrey*, *Kent*, *Somerset*, *Gloucestershire*, *Berkshire*, *Oxfordshire*, *Cambridgeshire*, Essex, Norfolk, Suffolk, Worcestershire, Herefordshire, Shropshire, Warwickshire, Staffordshire, Nottinghamshire, Lincolnshire, Derbyshire, *Cheshire*, Lancashire, Yorkshire, Cumberland.

Wales: Glamorganshire, *Pembrokeshire*, Denbighshire, *Merioneth*, Flintshire.

Scotland: Berwickshire, Edinburgh, Haddingtonshire, Fifeshire.

Ireland: *Cork*, *Tipperary*, *Clare*, Dublin.

REFERENCES

Beresford, D. R. Pack (1926). 'A list of the harvest-spiders of Ireland.' Proc. R. Irish Acad. 37B: 125–40.

Bristowe, W. S. (1935). 'The spiders of Skokholm (S. Wales), with Notes on a Phalangid new to Britain.' Proc. Zool. Soc. Lond.: pp. 233–9.

Bristowe, W. S. (1941). 'The comity of spiders.' 2: pp. i–xiv + 229–560. London.

Cambridge, O. Pickard- (1890). 'On the British species of Phalangidea or harvestmen.' Proc. Dorset Nat. Hist. Fld. Cl. 11: 163–216.

Muffet, T. (1658). 'The theater of insects', in Topsel, E., 'The history of four-footed beasts and serpents.' London.

Pickard-Cambridge, O. (1897). 'British Arachnida observed and captured in 1896.' Proc. Dorset Nat. Hist. Fld. Cl. 18: 108–15.

Roewer, C. F. (1923). 'Die Weberknechte der Erde.' Jena.

Savory, T. H. (1938). 'Notes on the biology of harvestmen.' J. Quekett Micr. Club, Ser. 4, 1: 89–94.

Savory, T. H. (1948). 'Synopses of the British Fauna. No. 1. Opiliones (Arachnida) or harvestmen.' 2nd ed. Linn. Soc. Lond. pp. 1–19.

Todd, V. (1948). 'Key to the determination of the British harvestmen (Arachnida, Opiliones).' Ent. Mon. Mag. 84: 109–13; and separate reprint, London.

THE STATISTICAL ANALYSIS OF THE SUNSPOT AND LYNX CYCLES

By P. A. P. MORAN
Institute of Statistics, University of Oxford

(With 1 Figure in the Text)

The regularity and stability of the 'ten-year' lynx cycle in Canada, as revealed in the numbers trapped by the Hudson Bay Company (Elton & Nicholson, 1942) naturally raised the question of it being in some way causally connected with the sunspot cycle. This question has been answered in the negative (Elton & Nicholson, 1942; MacLulich, 1937) and as appears from a careful examination of the figures, rightly so.

However, in view of the extremely interesting nature of these two series it may be worth while to set out here the criteria by which such a question must be decided, particularly in view of the fact that the correct application of statistical theory to such a problem is not at all widely understood.

In Fig. 1, I have graphed Wolfer's sunspot numbers from 1820 to 1934 and the common logarithms of the numbers of lynx caught in the Mackenzie River district of the Northern Department of the Hudson Bay Company (or its equivalent modern area). The sunspot numbers were taken from Yule (1927) for the period 1820–1924 and from the *Monthly Weather Review* for 1925–34. The lynx numbers were taken from Elton & Nicholson (1942) and the Mackenzie River district values were chosen because they gave an uninterrupted sequence from 1820 to 1934, and because taking the values for a single district results in a greater regularity in the cycle. Because of the extremely large values at each peak the common logarithm was taken in order to stabilize the oscillations. The ordinary correlation coefficient between these two series,

$$r = \frac{\sum_1^n (x_i - \bar{x})(y_i - \bar{y})}{\{\sum_1^n (x_i - \bar{x})^2 \sum_1^n (y_i - \bar{y})^2\}^{\frac{1}{2}}},$$

where $\bar{x}$ and $\bar{y}$ are the means of the sets of values $(x_1, \ldots, x_n)$, and $(y_1, \ldots, y_n)$, was found to be 0·1329.

MacLulich (1937) carried out a similar calculation (without taking logarithms) on series based on different data. His conclusion that the two cycles are not causally connected is certainly correct, but he reaches it by making a test of significance on the resulting correlation coefficient and in doing so commits a double error. He says (1937, p. 101): 'If the coefficient is less than the probable error there is no correlation and if it is greater than six times its probable error there is definite correlation.'

In the first place, if the test of significance is valid, significance is attained at the 5% level when the coefficient exceeds 2·91 times its probable error, and at the 1% level when it exceeds 3·82 times its probable error. His limits of significance are therefore too wide. The probable error, a number not now in common use because of certain theoretical reasons, is obtained by multiplying the standard error by 0·6745.

But in any case the test of significance is not valid here. Given any set of pairs of values

$$(x_i, y_i)\ (i = 1, \ldots, n)$$

a correlation coefficient can be calculated and is a valid descriptive measure of the way in which the two series of numbers vary together. But we also usually wish to test the significance of such a coefficient, i.e. to answer the question whether as large or larger a value could have been obtained by chance alone. To do this by the usual methods we must assume that different pairs are independent of each other so that the n pairs may be regarded as a random sample from bivariate population in which the variates are independent. But this condition is not at all true in the present case. For consider (x_i, y_i) and (x_{i+1}, y_{i+1}). Then x_{i+1} is much more likely to be near x_i in value than a randomly chosen x from the whole series, and similarly for y_i, y_{i+1}. We express this by saying that the series $\{x_i\}$ and $\{y_i\}$ are serially correlated in themselves. This fact completely invalidates the above method of testing the significance of the correlation coefficient.

The mathematical problem of setting up a test of significance in such circumstances is one of great difficulty. It may be shown, however (Moran, 1947), that for long series the standard error of the correlation coefficient is approximately equal to the square root of

$$n^{-1}(1 + 2\sum_1^\infty \rho_s \bar{\rho}_s),$$

where n is the length of the series and ρ_s, $\bar{\rho}_s$ are the serial correlation coefficients of the two series. The estimation from the data of these serial correlation coefficients itself presents considerable difficulties.

An account of their use in investigating the structure of a series will be found in Yule (1927), and there is a considerable literature on their estimation in recent papers in *Biometrika*, and in the *Journal* and *Supplement of the Royal Statistical Society*. See also Moran (1947). A coefficient may be considered to be significantly different from zero at the 5 % level if it is known that its distribution is approximately normal, about zero mean, and if it exceeds twice its standard error.

In general most time series are of such nature that the presence of the serial correlation coefficients in formula (1) results in the standard error being larger than would be the case if the successive pairs of observations were independent. In the present case $r = 0{\cdot}1329$, which would not be considered significant at the 5 % level if successive pairs of observations were independent. It would therefore be very unlikely to be judged significant by the more exact test using formula (1). The above described error of testing the significance of a correlation coefficient by ordinary methods when successive pairs of observations are not independent is so common in economic and other writing (e.g. Beveridge, 1944, Appendix D, p. 410) that it seems valuable to direct attention to it.

Although statistically significant correlation cannot be deduced from the data in Fig. 1, we can, nevertheless, say, on the other hand, that the possibility of sunspots being a major factor in causing the lynx cycle is decisively ruled out. For the oscillations of the latter are so regular that they cannot be explained by another regular cyclical phenomenon with which it is clearly in phase at some times and out of phase at others. Thus from 1820 to 1850 the cycles are very nearly in phase, whilst from 1850 to 1890 very nearly in opposite phase and so on. The regularity of the oscillation in both cases is so great that it is clear that there can be no causal relation between the two series.

Although not quite relevant in the present problem, two other sources of fallacy in the treatment of correlation between such series deserve mention. In the first place if there exist trends in the two series, large positive or negative correlations are to be expected but are not to be regarded as evidence of causal connexion, for clearly any two phenomena which show a pronounced trend throughout time will give such high values when correlated together.

Another common procedure when looking for causal connexions between such series is to lag one series one, two, or more units of time with respect to the other and calculate a correlation coefficient for each lag, picking out the largest. This may give suggestive results but once again the test of significance is invalidated, because we have chosen the largest of a set of correlation coefficients.

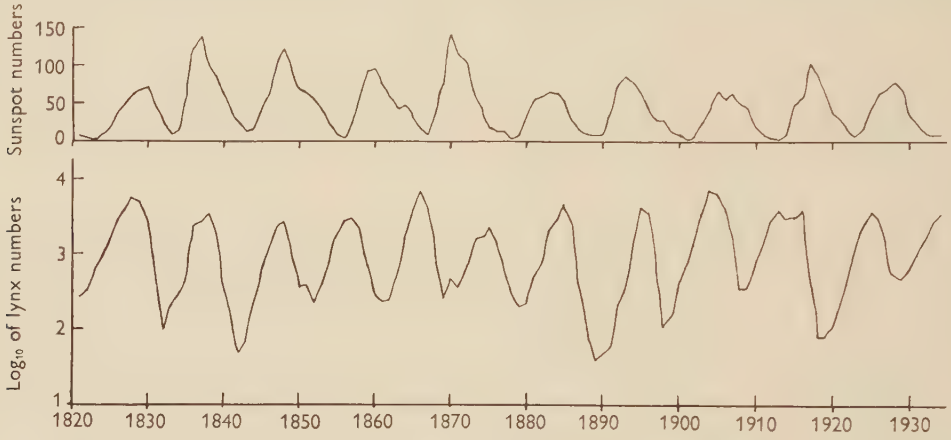


Fig. 1. Cycles in numbers of sunspots and trapped lynx.

SUMMARY

The statistical testing of correlation between cyclical time series is discussed. The fallacy of applying the ordinary test of significance to the correlation coefficient between series which are not serially independent in themselves, is pointed out, and other sources of fallacious conclusions mentioned. Examination of the sunspot and Canadian lynx cycles, however, rules out the possibility of a causal connexion between them.

REFERENCES

Beveridge, Lord. (1944). 'Full employment in a free society.' London.

Elton, C. & Nicholson, M. (1942). J. Anim. Ecol. 11: 215–44.

MacLulich, D. A. (1937). Univ. Toronto Stud. biol. 43: 1–136.

Moran, P. A. P. (1947). Biometrika, 34: 281–91.

Yule, G. U. (1927). Philos. Trans. A, 226: 267–98.

SPECIAL REVIEW

POPULATION CHANGES IN GERMAN FOREST PESTS

By G. C. VARLEY

(With 1 Figure in the Text)

F. Schwerdtfeger (1935). 'Studien über den Massenwechsel einiger Forstschädlinge'. Z. Forst- und Jagdw. 67: 15–38, 85–104, 449–482, 513–540.

F. Schwerdtfeger (1942). 'Uber die Ursachen des Massenwechsels der Insekten'. Z. Angew. Ent. 28: 254–303.

Census work on certain insect pests of the German State Forests has been continued for a total of 60 years, and the results are of very great interest to ecologists. An important account was published in 1935, and this was followed by a further review in 1942. The data concern the population densities of four species of moths, all of which feed as larvae on the needles of the pine *Pinus sylvestris* L. The populations were estimated annually in December by counting pupae or larvae in the surface soil of selected localities. The results are given by Schwerdtfeger as graphs of the numbers found per 100 sq.m. Since the population densities varied between 0·1 and 2500 per 100 sq.m. the direct plotting employed by Schwerdtfeger has disadvantages. His data from Letzlinger Heide have therefore been read off his graphs, or taken from the actual figures where these have been given, and have been replotted on a logarithmic scale. This has the advantage that the enormous peaks of population are easily plotted on the same graph. Also relative changes in population density show clearly at all population densities. The very lowest values were difficult to read accurately from the original graphs, but any inaccuracies introduced here by the reviewer are of small importance, as the statistical errors are also very large when the population density is estimated to be as low as 1 per 1000 sq.m.

Panolis griseovariegata (Goeze), pine beauty, Noctuidae. (Called by Schwerdtfeger the Eule, or Forleule, *P. flammea* Schiff.). This species showed small peaks of population density in 1883, 1888, 1893 and 1897, which begins to suggest regular oscillations with a 5-year period. But oscillations apparently ceased between 1899 and 1910, when changes were rather small and irregular. In 1912 there was a definite peak, when the population density reached its maximum value of 40 per 100 sq.m. Further peaks in 1919 and 1931 led up to the much larger populations between 1937 and 1939.

Hyloicus pinastri (L.), pine hawk, Sphingidae (Kiefernschwärmer, *Sphinx pinastri*). The data for this species were omitted by Schwerdtfeger in his 1942 paper, and have been taken from his paper of 1935, which gives data only up to 1930. The population change from generation to generation in this species was rarely as great as fourfold, and was often much less. Also the population density tended to remain rather low. Only in 1887 did its population density rise as high as 38 per 100 sq.m. This peak, and smaller ones in 1899, 1915 and 1927 all coincided with periods when the population of *Bupalus* was also high.

Dendrolimus pini L. (Kiefernspinner) is a large Lasiocampid moth, not found in Britain. It was seldom a pest at Letzlinger Heide and had only two major outbreaks (gradations) during the period. In the outbreak of 1886–9 the population density rose to a maximum of 18 per sq.m., and in 1937 it rose to 3 per sq.m. From 1890 to 1927 the population remained below six larvae per 100 sq.m., and was often far below this. Two minor peaks of population density in 1927 and 1932 suggest increasing oscillations with a 5-year period, leading up to the major outbreak of 1937.

The picture for *Bupalus piniarius* (L.), bordered white, Geometridae (Kiefernspanner) is quite different from the other species considered. Letzlingen is in the centre of the main area of damage by this species, and outbreaks were both frequent and severe. Never did the population density settle to an approximately steady state, as sometimes happened with the other three species. Seven small or large outbreaks were recorded in the period of observation: in 1888, 1894, 1900, 1905–6, 1917, 1928, and 1936. Up till 1905 there were peaks of population density every 5 or 6 years. Then there were gaps of 12, 11 and 8 years.

Schwerdtfeger's two papers are largely devoted to detailed discussions of the causes of the striking population changes observed. In the earlier paper the

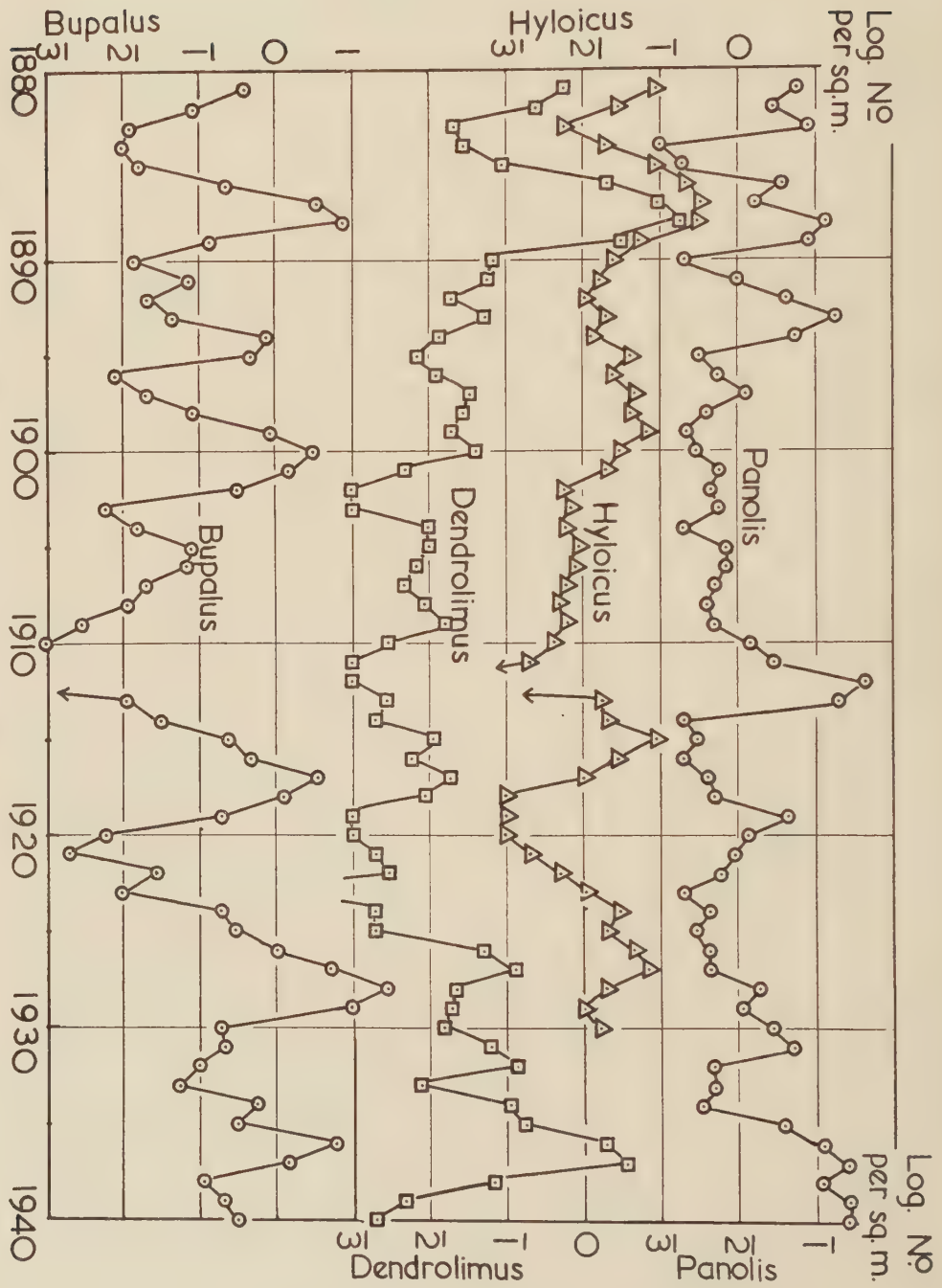


Fig. 1. Results of 60 successive winter census counts of moth pupae (or in the case of *Dendrolimus* hibernating larvae) per square metre of forest floor at Letzlingen, Germany, replotted on a logarithmic scale.

data are analysed in relation to a theory of *gradations*. Between gradations the population is in a kind of dynamic equilibrium, and fluctuates up and down at a low level, termed the 'normal Bestand', or less appropriately the 'eiserne Bestand'. The upper limit of this 'normal' population density is defined as 10 per 100 sq.m. for *Bupalus*, and 5 per 100 sq.m. for the other three species. Below this limit of the 'normal Bestand' Schwerdtfeger points out that 40-fold changes in the population density can occur. These changes show very clearly when the data are plotted, as in Fig. 1, on a logarithmic scale. When plotted as numbers on a normal scale such that the tops of the peaks can be shown on the graph, points within the limits of the 'eiserne Bestand' are so near the zero line that a superficial appearance of stability is given. How far this method of plotting has been responsible for the popularity of this theory in Germany and elsewhere is open to speculation.

If the population density should increase above this limit, it is supposed to be in equilibrium no longer, and a gradation begins. The population rises for a few years at a great rate, and a serious outbreak of the pest is the result. For reasons which seem obscure, Schwerdtfeger divides the gradation into four phases, two of increase, and two of decrease, and tabulates for each species the number of generations spent in each phase, and the number of years between each gradation.

The basic causes of the changes are not explained, but they are discussed in considerable detail in the 1942 paper. It must be said at the outset that a proper understanding of such changes requires reasonably complete knowledge about the mortality and fertility of the species. For certain years of exceptional insect abundance Schwerdtfeger does indeed give most of the data required for some of the species. On p. 286 of the 1942 paper the mortality and fecundity of *Panolis* are given for four different localities for one whole season. Had there been comparable data for a whole gradation some at least of the fundamental problems of population ecology might have been far better understood.

It is a pity that such valuable work should suffer from a serious omission of this kind; but this is unfortunately rather characteristic of ecological work at the present time. The cause in this case is not far to seek. Only when an insect is exceptionally abundant can data be easily accumulated. At the low population densities, of the order of 1 per 100 sq.m. or less, Schwerdtfeger very naturally found it quite impossible to get enough material for study.

In the absence of this crucial information Schwerdtfeger (1942) brings forward much other relevant data from the literature (mostly German papers, many of which are not readily available in this country) and reviews at some length the various theories which have been advanced to account for such population changes.

(*a*) *Parasite and biocoenosis theories*

By the parasite theory is to be understood the idea that specific parasites alone are responsible for population changes. Schwerdtfeger rightly considers this view far too simple, although it is well known that a high percentage of pests are at times destroyed by parasites, and that parasites have been successfully used in biological control. He emphasizes that since many parasites have a variety of alternative hosts, the whole biocoenosis must be considered; but that even this is not enough.

(*b*) *Weather theory*

Schwerdtfeger examines in detail the possibility that climatic factors may be responsible for the changes in population from year to year, and finds the evidence against this view. Bodenheimer's claim that in general climatic factors cause a mortality of 85–90 % in the egg and larval stages of insects is shown to be untrue for *Panolis*, in which this mortality was estimated to be as low as 25 %.

(*c*) *Overpopulation theory*

Eidmann's idea that in its main area of damage a pest shows regular outbreaks every 10–12 years is examined. Eidmann's figures were obtained from a variety of insect pests, such as locusts in South America, and *Dendrolimus* at Schweinitz in Germany. Originally, in 1931, Eidmann had interpreted these results in terms of the well-known 11-year sunspot cycle. Later (Eidmann, 1937) he abandoned this view, and explained them in terms of overpopulation. When for a number of years the population increases, the trees are eventually defoliated, food supply is reduced, and the pest brings about its own destruction by the reduction of its 'Lebensraum'. The critical factors here are reduced fertility, reduced resistance to disease, and death from starvation. These factors are density dependent. On this view no outbreak should come to an end without severe defoliation of the trees. But the data in Fig. 1 show various small peaks of abundance, such as that of *Panolis* in 1919, and *Bupalus* in 1905, which are far too small for this explanation to be tenable.

(*d*) *The factors of population dynamics*

Under this heading there is a very long discussion of factors which influence sex ratio, fertility and mortality, from which the following conclusions emerge:

(1) In no case is any single factor predominant, as

is suggested by the parasite theory, or the weather theory.

(2) Many factors operate, and each changes widely in its intensity from year to year.

(3) Factors may be either biotic, or abiotic. Hence neither parasite theory nor weather theory can be accepted alone.

(4) The importance of any single factor changes with time, place, species, etc.

(5) The only common factor is the variability of the factors which cause the population changes.

Thus, after a useful critique of a number of theories, Schwerdtfeger seems to relapse into obscurantism.

(*e*) *The gradocoene*

The changes in population density have been interpreted by Friederichs as due to the operation of the '*holocoene*' (Holocön), defined as the sum total of environmental factors of all kinds. Schwerdtfeger rightly regards this concept as too wide, since neither *all* species of the community, nor *all* the attributes of the physical environment have any significant effect on the numbers of one species. Only a part of the holocoene, called the *gradocoene*, is important. The gradocoene is the sum of the factors which affect the numbers of the species. That the gradocoene is therefore responsible for changes in the numbers of a species would appear to be a truism; but it is a point which perhaps needs emphasis, as it seems sometimes to be forgotten.

However, for Schwerdtfeger the gradocoene seems to have some mystic significance, and is a system of factors which regulate themselves to form an organized unit. The pest itself is regarded as the centre of an organized network, which strives to reach equilibrium. Nevertheless, it is clear from the data that stability is not achieved.

The cause of gradations remains obscure. Impressed by the big changes even when population densities are low, Schwerdtfeger suggests that a gradation is merely an unusually strong swing of the ever-moving pendulum of population density. But the changes are by no means random. Periods in which there is population increase for a number of years are followed by almost equally long periods of decrease, as is particularly clear for *Bupalus*.

Nowhere in his papers does Schwerdtfeger make any use of statistical methods, either to estimate the variance of numerical data, or in other ways. Yet various questions quickly come to mind which can profitably be studied in this way. For instance, examination of Fig. 1 shows that the peaks of abundance of *Dendrolimus* and *Bupalus* often seem to be coincident or nearly so. Are the numbers of these two species correlated? Calculation shows that the correlation coefficient is $r = 0{\cdot}20$, with a probability of between 0·1 and 0·2 that the observed degree of correlation is due to chance. Similarly, the correlation coefficient between the numbers of *Bupalus* and *Hyloicus* has been found to be $r = 0{\cdot}18$, with a probability of 0·2 that the resemblance might be due to chance. Moran (1949) has shown that correlation coefficients calculated in this way from oscillatory time series may easily give misleading high values of significance. But as the correlation is low, the data lend no support to the view that a common factor may be responsible for the changes of more than one species.

Various broad ecological issues raised by these long-continued observations are hardly touched on by Schwerdtfeger. Here we have four species of moth, each belonging to a different family, all living together and eating the same food. Under the simplest conditions of interspecific competition for food, only one species should survive (Gause, 1934); and this has been confirmed experimentally *in vitro* by Crombie (1947) and Park (1948). What are the conditions which permit the continued coexistence of four species in nature?

It might be that Letzlingen is a place where two or more geographically separated species, each adapted to a different climate, happen to find conditions equally suitable, and hence overlap in just this region. The climatic requirements of the species have been studied in detail by Schwerdtfeger (1935), and are in fact very similar, although the localities where *Dendrolimus* is a major pest tend to be slightly warmer and less humid than those where other species thrive. *Panolis* and *Bupalus* are major pests in areas of identical mean monthly temperature, humidity and precipitation, except that *Panolis* seems most abundant where April temperatures are higher. It is then that this moth is on the wing. Schwerdtfeger (1935, fig. 10) gives a map of the areas of damage of the species, and there is little or no difference in their distribution. The evidence gives no support at all to the idea that Letzlingen is a unique locality where separate areas of distribution happen to meet.

Another possibility lies in the fact, which Schwerdtfeger hardly mentions, that the life cycles of the four species are different. This is shown in Table 1, based on information in Spuler (1908–10), where l indicates small and L fully grown larvae.

The main emergence periods of the moths varies between April for *Panolis*, and July for *Dendrolimus*. The weather conditions during the adult stage, in which mating and oviposition occur, must be very critical for each species. Heavy rain or high winds might also cause heavy mortality in the very small larvae. The differences between the species is so great that their individual critical periods scarcely overlap at all. This isolation in time is the sort of thing to be expected as a mechanism preventing the inter-

Table 1

	Apr.	May	June	July	Aug.	Sept.	Oct.	Winter
Panolis	Moth Eggs	l	l	L L	Pupa.....			
Hyloicus	Pupa.....			Moth Eggs	l	L	Pupa	
Bupalus	Pupa	Moth Eggs		l	l	L	L	Pupa.....
Dendrolimus	l	L	Pupa	.....Moth	Eggs	l	l	Hibernating

breeding of closely allied species, but cannot be supposed to have this function here. On the other hand, Lack (1944) has shown that closely allied species of birds can live together if they are of different sizes, and therefore take rather different foods. Is it possible that competition between species is reduced if their feeding and growing stages are of different sizes at the same time, which is one result of the differences between the life histories?

Schwerdtfeger gives no clear picture of the extent to which the four species compete for food. Defoliation certainly occurs in the worst outbreaks, but which outbreaks caused defoliation and which did not is not clearly stated. But food supply was at times limiting, and a footnote to Schwerdtfeger's table 2 (1942) states that adults of *Panolis* migrated away from a defoliated area in 1932.

The effects of defoliation on the pine is much more severe than on a deciduous tree such as oak, which puts forth new leaves in the same season. Marcus (1942) shows photographs of sections of pine trees which had been heavily damaged by an outbreak of *Panolis* between 1928 and 1930 in another area. They show a minute growth ring in 1930, none at all in 1931 or 1932, small rings in 1933–5, and the first year of normal growth was 1936. This disastrous effect on tree growth is related to the fact that each pine needle normally lives for 3 years before it drops. New leaves are not immediately put forth after defoliation, and a full series of new leaves will require at least 3 years to grow.

When the trees are defoliated the various species of caterpillar presumably compete for the reduced food supply. The increase of one species to abundance may then inhibit the increase of another. Perhaps this may explain some of the small peaks of *Hyloicus* when *Bupalus* was already far more abundant. But other factors must be at work, since none of the species was at all abundant between 1903 and 1911, and there was no major outbreak, and hence no likelihood of defoliation, between 1890 and 1925. The four species compete for a limited amount of food only on rare occasions.

The most likely hypothesis to explain the coexistence of the four species is that the population densities of each species are separately controlled by different factors at such low population densities that direct competition for food is very uncommon. The parasites of the caterpillars may be the main factors. Schwerdtfeger gives an inadequate idea of the position, but the parasite catalogue of Thompson (1943–) gives useful lists. Neglecting the records for 'Europe' and taking only those for Germany, one finds 33 species listed as parasitic on *Panolis griseovariegata*, 26 of which have not been recorded from the other three hosts. Of the 19 species parasitic on *Bupalus piniarius*, 13 are not recorded from the other three hosts. Two of the four species on *Dendrolimus pini*, and three of the four species on *Hyloicus pinastri* do not attack the other species. No species of parasite was found on all four hosts, although the ubiquitous egg parasite *Trichogramma evanescens* Westw. and the chalcid *Dirhicnus alboannulatus* Ratz. each attacked three hosts, and five species of parasite attacked two hosts.

Clearly the different species of hosts are to a very large extent attacked by effectively specific parasites. If these parasites are the agents responsible for the control of the population density of the pests (and one is left in doubt as to how far this may be so by the lack of data) then the numbers of each of the four species may be controlled independently. The only common factors would be general predators such as birds, and occasional food limitation when one or more of the four species happened to have an outbreak.

There is some indirect evidence that parasites themselves may be responsible for the gradations. Schwerdtfeger shows that the catastrophic fall of the population at the end of a gradation is accompanied by a very high percentage of parasitism, if it is not indeed so caused. This amounted to 98·5 % parasitism by tachinid flies at the end of a gradation of *Panolis*. Details are given also for *Dendrolimus* between 1934 and 1935 at Malterhausen where in two successive generations the percentage of parasitized pupae rose from 20 % in 1934 to 58 % in 1935, and was accompanied by a heavy fall in population. Unfortunately there are no data about the percentage of parasitism when the population density is rising from very low values. The theory of Nicholson & Bailey shows that regular oscillations in population density may be expected if a species is controlled by a specific parasite. The percentage of parasitism is very low as the host increases, and rises to very high values as the population falls.

Furthermore, Nicholson & Bailey (1935, p. 585) give a formula for the period of the oscillations in the population of host and parasite, the value of which depends solely on the rate of increase of the host in the absence of the parasite. The figures below have been computed from this formula:

Rate of host increase per generation	1·5	2·0
Period of oscillation in generations	10·2	8·2

3	4	7	10	20	100
7·0	6·3	5·6	5·4	5·0	4·7

These figures are valid only for oscillations of small magnitude. If the amplitude is large, then the period of oscillation is longer, so that the change in population can be achieved with unrestricted increase of the host in half the period of oscillation.

It will be seen that the calculated period of oscillation is little affected by changes in the rate of host increase, once this is greater than fourfold. We shall not require a very accurate estimate of host increase to get a satisfactory estimate of the period of oscillation. For this purpose we do not require the mean number of eggs laid per moth, but the net rate of increase of the host with the effects of all mortality factors included, except the parasites. Assuming that the effect of the parasites can be neglected during periods of rapid host increase, this can be estimated from the data in Fig. 1.

For *Bupalus* the mean value of the net rate of increase per generation, when increase is rapid, is given by the antilog of $0{\cdot}85 = 7$, and estimates for the other species are similar, except for *Hyloicus*, which increases about threefold per generation. Hence, according to Nicholson & Bailey, the period of oscillation should be between five and six generations for three of the species, and about seven generations for *Hyloicus*, always assuming that the effective parasite in each case has one generation to each generation of the host.

At various times *Dendrolimus*, *Panolis* and *Bupalus* show three or four consecutive peaks of population indicating oscillations of about this period. But there are also times in which there are oscillations of a much longer period (e.g. the very strong swings of population in *Bupalus* after 1905), or no sign of oscillation at all, as is the case for three of the species between 1895 and 1910.

Where the change in population density is small, can it be that it is close to the *steady density* of Nicholson? If this were so, once oscillations restarted, the population density should rise above and then fall below the previous level. Examination of the curves in Fig. 1 gives no support to this idea. Thus *Dendrolimus* remains at a low population density from 1901 to 1925 and then shows three clear peaks, the first two being 10 times and the last 100 times the previous maximum. But the minima in between are well above the average of the previous period of low density. There is something happening here which does not fit with the theory of Nicholson and Bailey.

Superficially at least the attempts of Schwerdtfeger, and later of Voûte, to explain the long periods of low population density as a stable state, and to find separate explanations for the onset and ending of gradations are attractive. And this present attempt to see how far the facts can be explained in terms of Nicholson's theory meets with no more than partial success. But the nature of the data on which interpretation must be based remains inadequate. Let us hope that further work will be concentrated on producing the detailed mortality and fertility data which may eventually help to provide a proper explanation of these fascinating problems.

REFERENCES

Crombie, A. C. (1947). 'Interspecific competition.' J. Anim. Ecol. 16: 44–73.

Eidmann, H. (1931). 'Zur Kenntnis der Periodizität der Insektenepidemien.' Z. Angew. Ent. 18: 537–67.

Eidmann, H. (1937). 'Zur Theorie der Bevölkerungsbewegung der Insekten.' Anz. Schädlingsk. 13: 25–6, 47–52.

Gause, G. F. (1934). 'The struggle for existence.' Baltimore.

Lack, D. (1944). 'Ecological aspects of species-formation in passerine birds.' Ibis, 86: 260–86.

Marcus, B. A. (1942). 'Über das Wachstum der Kiefer nach starkem Eulenfrass.' Z. Angew. Ent. 29: 31–84.

Moran, P. A. P. (1949). 'The statistical analysis of the sunspot and lynx cycles.' J. Anim. Ecol. 18: 115–16.

Nicholson, A. J. (1933). 'The balance of animal populations.' J. Anim. Ecol. 2: 132–78.

Nicholson, A. J. & Bailey, V. A. (1935). 'The balance of animal populations. Part 1.' Proc. Zool. Soc. Lond. 551–98.

Park, T. (1948). 'Experimental studies of interspecies competition. I. Competition between populations of the flour beetles *Tribolium confusum* Duval and *Tribolium castaneum* Herbst.' Ecol. Monogr. 18: 265–307.

Smith, H. S. (1935). 'The rôle of biotic factors in the determination of population densities.' J. Econ. Ent. 28: 873–98.

Spuler, A. (1908–10). 'Die Schmetterlinge Europas.' Stuttgart. 3 vols.

Thompson, W. R. (1943–). 'A catalogue of the parasites and predators of insect pests.' Belleville, Ontario.

REVIEWS

ECOLOGY IN POLAND

Kazimierz Demel (1948?). *Zwierze i jego srodowisko.* (*Wstep do ekologii zwierzat.*) [*The animal and its environment.* (*An introduction to animal ecology.*)] Library of Knowledge, Vol. 50. 421 pp., 162 illustrations. Warsaw: Trzaska, Evert and Michalski.

This book, as the author says, is the first attempt to give a general representation of facts and principles of animal ecology in the Polish language. Although ecology as a special branch has been discussed in pre-war Poland only in essays and short articles, yet ecological methods were used in many zoological investigations.

It is not mere coincidence that the author, who works at the Marine Station at Gdynia, is a hydrobiologist. This field of ecological research flourished in a country richly endowed with fresh-water basins. Terrestrial ecology was less advanced but vegetation studies flourished specially in Cracow and Lwow and a text-book on the 'Ecology of plants' (Szymkiewicz, 1932) was based to a great extent on local studies. In the great struggle to heal the ravages of war on Polish science much attention is paid now to the publication of text-books and books of general reading on scientific subjects. Dr Demel's book is designed to give information to the general public on ecology, which the author defines as the 'economics of animal life in the framework of nature'. In eight parts the book deals with the main topics as: water and land as environments; climatic, edaphic and biotic factors; main types and principles of animal association; classification of habitats in ocean, fresh water and land; man as ecological factor. It seems fitting that there should be two chapters devoted to the preservation of nature and natural resources, in a country in which these aims had always a strong appeal.

It is to be hoped that future editions will show an improvement in the selection and the standard of illustrations, which at present seem to have been chosen partly because they were at hand. It would be desirable also that more space should be devoted to local conditions. If ecological research in Poland is to be fostered, a text-book based to a great extent on easily accessible habitats and animal associations would be highly desirable. Efforts should be made to publish Alfred Litynski's book on Hydrobiology, based largely on original research and treating Polish waters.

Demel's book is a most desirable step forward; it is fully adequate to fulfil its mission as a stimulating book of general reading.

J. RZÓSKA

ALPINE COMMUNITIES

H. Franz (1943). *Die Landtierwelt der Mittleren Hohen Tauern: ein Beitrag zur Tiergeographischen und Soziologischen Erforschung der Alpen.* Denkschriften der Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse, 107: 552 pp., 14 plates, 11 maps.

Those who remember a paper (1939, Biol. Rev. 14: 369–98) by Dr Franz, in which he advocated the abandonment of the 'biocenosis' as a working unit in animal ecology and the employment of the 'association' (defined by the constant presence of characteristic species) will welcome the present work as a practical testing-out of his theoretical ideas. It may be with some surprise that they discover this to take the form of 552 large pages of small type discussing the distribution of 4411 species between 270 stations; but herein lies the work's second main claim to the attention of the ecologist as a basic study which will be used in all future studies of Alpine faunas.

An attempt is made to cover the entire animal kingdom, but the Protozoa have—reluctantly—been omitted from the study; even so we must admire the persistence of the author in distributing the vast material to so many taxonomic experts (a most useful list of whom and their works is included in the paper) and for collating their results.

The Hohen Tauern are the final eastern outposts of the Alps, lying east-south-east of Innsbruck and grouped round Grossglockner (12,461 ft.). This mountain is at the centre of the large area under study, which is almost entirely 'high alpine' in nature. Geographical, geological and climatic data are given and show that there is an immense range of environmental conditions in the area, dependent especially on altitude and aspect. The higher localities have a mean temperature above zero for about two months of the year; those around 700 m. for the same period are above 15° C. and show a difference between lowest and highest monthly means of 23° as opposed to 13° C.

It is hardly surprising, therefore, that the fauna shows a great range of types and a total number of species which, in most taxonomic groups, is about one-fifth that of the entire British fauna. Among the insects outstanding exceptions to this ratio are Orthoptera and Plecoptera (about as many species as in the British fauna), and Ephemeroptera (1 species) and Vertebrata (1 fish, 3 Amphibia, 4 reptiles, 18 birds and 10 mammals) which are very poorly represented.

It would appear to be a common experience in ecological survey work of this kind that, rather than being able to collect data in a manner most suitable for the main object or problem concerned, we are presented with a mass of rather disconnected data and have to do the best we can about systematizing it; this is rather the impression given by the work under consideration. There could hardly be a greater contrast than between this paper and Agrell's (1941) on Lapland Collembola, for instance, but both authors are attempting to do the same sort of thing—to divide a region up into districts which correspond with marked differences in the species composition of the fauna. Agrell's study was limited to a single group of animals, Franz's is much more inclusive, which makes it more difficult to employ comparable sampling methods for all types. In his 'declaration of principles', mentioned at the beginning, he stated that determination of sociological affinity should be based on 'an approximate

quantitative census of simple areas of equal dimensions'. In practice, even this seems to have been abandoned and mere presence or absence, except in the rather sparsely sampled and very variable soil communities, are the only records made.

The division of the area into 'associations' is, in the first place, based almost entirely on the plant associations defined by botanists working in the district, although a rather greater number of animal associations can be detected by using the criterion of the constant occurrence of characteristic species. The method is, therefore, quite admittedly 'subjective', even in comparison with Agrell's studies. The nature of the material does not allow the use of quantitative sampling or measurement of abundance, dominance or constancy, although the latter is divided into the subjective categories of Braun-Blanquet's 'Gesellschaftstrue'.

The question to which the ecologist will demand an answer is whether the present type of investigation can be as valuable as the more detailed and time-consuming statistical type, or whether elaborate sampling methods offer any advantages. It should first be pointed out that the latter have been applied on a large scale as, for instance, in Krogerus's monumental work on the Finnish sand-dune faunas (R. Krogerus, 1932, Acta Zool. Fennica 12: 1–308). Although only about one-third the number of species was involved, this author was able to determine frequency, dominance, abundance and constancy of the various species involved and to arrive at valuable generalizations about the different species and biotopes. It remains uncertain, however, to what extent such a study can enable one to compare numbers of animals which inhabit different vertical layers, different media and are active at different times and seasons despite their habitats being interspersed in what appears to be the same area.

The important question is whether, with all this extra work, Krogerus was able to find out things about his region which Franz could not have done, and the answer is definitely in the affirmative. However, the range of environmental factors was so much greater in the Hohen Tauern than on the sand dunes that the majority of faunistic differences were much more distinct; species having clearly defined limits so that exact quantitative measurements were less necessary. It seems most probable, however, that, should a more quantitative material be obtained within any one of the major zones, or even of the associations of Franz's study—a type of study which he recognizes as being most necessary—then the existence of a whole range of further 'associations' would probably be revealed by the application of suitable methods; although the greater range of habitat types would make this correspondingly more difficult.

It would appear, therefore, that in the initial stages of an extensive inquiry of this sort general records and 'subjective' grouping into communities and the wide experience of the natural history of the region which results from constant work there can allow one to make useful divisions into faunistic types but, whether such groupings are the ultimate animal associations is very doubtful.

One generalization to which Franz is led by his results is the very great difference in ecological tolerance shown by the members of different taxonomic groups. Beetles and mites, for instance, appear to be distinctly 'eurytopic', while the Nematoda and Enchytraeidae are very widespread and the species occupy much 'broader' niches. This seems to be connected with the general physiological tolerance of the groups concerned; the nematodes, for instance, being very resistant to adverse environmental conditions, while beetles tend to be more restricted to very specialized habitats both as regards microclimate and food. Perhaps, too, such characteristics are connected with the superior mobility of individuals of the more specialized groups, but this tendency for whole phyla to exhibit similar tolerance ranges has not, apparently, been pointed out before.

The paper ends with a section on the zoogeography of the region and shows that, although there are a number of relict forms, the vast majority of the fauna which existed there during warmer, post-glacial times has been wiped out and replaced by immigration, mainly from the East.

The whole survey was made under the Deutschen Alpenvereins and indicates that valuable work on pure science certainly was accomplished during the war. As the author says, in an appeal for greater concentration of all types of investigation on synecological work, it is only by the adoption of such an attitude that we can learn 'to let nature work for us, instead of, as so frequently happens to-day, working against her and, as a result, employing much greater expenditure of money and work in the consequently prolonged struggle'. It would appear that such an attitude was not wholly foreign to the German authorities during this difficult period.

A. MACFADYEN

A CENTRAL JOURNAL OF NATURAL HISTORY

The New Naturalist: a Journal of British Natural History. 1948. [Four quarterly numbers bound into one annual volume.] 216 large quarto pp., many illustrations. Ed. **James Fisher and Elisabeth Ullmann.** Collins, 14 St James's Place, London. Price 21*s*.

Since the *Zoologist* stopped appearing a good many years ago there has not been any general journal of natural history in this country, although the *Scottish Naturalist*, *North Western Naturalist*, *Naturalist* and *London Naturalist*, and others devoted to particular regions, have kept up a worthy standard of general and varied interest. And even the *Zoologist* paid little attention to insects, leaving these to the entomological magazines. Genuine naturalists and ecologists have for some years felt the absence of a central channel for information and critical articles, since the popular magazines or sections of country journals have been often pitifully bare in facts and ideas, and have mainly kept out of the currents of ecological thought.

The Editors of the present venture state that they intend to make field studies of animals and plants (including questions of evolution) and of their environment in geography and climate the field of their interest,

and that the journal is to be informative but not, in the inferior sense, 'popular'. I think the price and the very high standard of beauty in printing and illustration in themselves lift it above the level of any existing periodical of natural history or country life; and the contents of the first annual volume justify full confidence in the intellectual level of the contributions. The only general criticism one might make is that the journal is almost *too* finely produced for the ordinary (and still humble) naturalist to feel quite comfortable, as he moves warily about among lovely photogravures of British scenery and almost life-size passerine birds, or sets his jaw to read through the large quarto pages of excellent print. But no doubt streamlining has come to natural history, as to motor-cars and teapots, and we must forget the days when it was sufficiently exciting to probe through the small-print notes of natural history items, or vault the hurdles ingeniously placed by secretive taxonomists to keep us from learning about animals. But one should not minimize the achievement of the Editors and Publishers in producing anything of the sort that combines so effectively critical and well-written general articles with lavish and on the whole very well-chosen illustrations. And only those who have tried to find appropriate pictures to exemplify some theme of writing or teaching can realize the practical obstacles that have been faced and overcome.

The correct answer to my criticism about the over-luxuriousness of the volume is probably the institution of a much smaller and less illustrated natural history journal of information, more pedestrian, more like the entomological magazines (which have a steady output of highly valuable material at a fairly low cost), general in scope of matter received but less concerned with interpretive writing. Such a periodical would not compete with the *New Naturalist* journal, but would, I think, find a valuable position as the barriers between different segregated disciplines are slowly eroded away by the activities of ecologists.

It is intended eventually to issue the *New Naturalist* as a quarterly journal, so the present volume is in the nature of a multiple birth. The first part circles about woodland problems: a map of management types and frequency for England and Wales; pre-history and pollen evidence; woodland communities (a précis by Prof. Tansley from his great book on vegetation); British species of elm with useful distribution maps; red and grey squirrel problems; woodland butterflies and their curious population fluctuations, spreads and retreats; titmice; and bird communities generally in woods.

Part II surveys aspects of the Western Isles of Scotland, and is the most dramatically illustrated: geography; climate; Heslop Harrison's Quaternary distribution ideas for plants and animals (here stated rather more succinctly than hitherto); some special animal groups such as grey seals, and Leach's petrel; the evacuation and subsequent ecological fate of St Kilda (by the Editor) and the general ecology of Ailsa Craig; and a note on the need for more effective bird protection.

Part III is concerned with migration as a problem, though the article on the corncrake really refers to historical spreads and fluctuations more than to migration as such. The articles in this part are somewhat less satisfying than the earlier ones, because one feels that much of the material is old ground that has been tramped over many times without further advance in interpretation. The study of migration, in fact, keeps getting lost in the foggy uncertainty about physiological mechanisms of periodic migration, even historical meanings of it, and always about direction finding whether in insects or birds. The articles sum up points about butterfly migration; bird orientation; goose movements; bird migration observation stations in this country; and bird-ringing. The maps are well drawn and informative.

The final section is a straightforward and valuable description of the position of natural history: its societies (including those of schools), journal and radio. The main feature is a long list of the existing societies under county headings, based on the *Directory of Natural History Societies* (which is an independent publication). Speaking as one who has searched through most of the publications of the lesser societies, I shudder when I think of the great quantity of almost rubbish that is published by some of them; there they are, however, and as has been said, all human happiness counts. And there are some excellent fires alight here and there, which will, one hopes, be noticed and encouraged by the *New Naturalist*, when it comes to a more critical sifting of their work.

This periodical deserves full support from those ecologists who can afford it, for they will get more than their money's worth, much knowledge that cannot be easily come by without great loss of time in searching, and undoubted pleasure not only in the beautiful production but in knowing that someone is trying to focus in one channel differently derived views and experiences of nature.

CHARLES ELTON

REGIONAL ECOLOGY

F. Fraser Darling (1947). *The natural history of the Highlands and Islands.* 45 coloured and 55 photogravure plates, 25 figures and distribution maps. Collins, 14 St James's Place, London. Price 16*s*.

This book surveys in a broad way the natural history of Scotland north and west of the Highland line, dividing it into areas characterized by physiography, land use and major habitat. The result is patchy, since the author's knowledge is not of equal standard for each section; some parts are very much 'written up' from the literature with the result that only the writing redeems them from dullness. This is probably inevitable, when an attempt is made to cover so large a field. For all that, it is a sincere and painstaking effort to give a coherent picture of Highland natural history in a more comprehensive way than has been done before. One of the most valuable and interesting parts of the book is the discussion of the status of various animals and plants against the background of land use and exploitation. The latter is generally known to have born hard on the Highlands, but it is difficult to find a work of this scope giving full details.

The opening chapters sketch the geology, climate and vegetation types of the whole area. This is not easy to follow for those who do not know the country because of the use of many obscure place-names and the inadequacy

of the maps. The fourth chapter opens the consideration of man's history in the Highlands and of the effects produced by his settlement; deforestation is discussed in all its sad detail together with the introduction of those two changers of the earth's surface, the sheep and the rabbit; the effect of such denudation upon the status of the most characteristic forest animals is assessed species by species.

Next are considered the vast stretches of deer 'forest' and hill grazings, which have in part arisen from the removal of trees, and the value and effects of the different interests concerned—sporting, pastoral and scientific—are evaluated with a notable degree of objectivity.

The following chapter on the life history of the red deer, and a later one on the Atlantic grey seal stand in a category of their own, because the writer is dealing with subjects which he has himself studied intensively, and these chapters, unfortunately, point the contrast with other sections, which do not rest upon the same first-hand knowledge. These last deal with the composition and distribution of the present forests, with life and climate above the tree line, with the ecology of the shores, lochs and river systems and with the divergencies in climate, vegetation and land use between the mainland and the islands. They all have flashes of stimulating information, but are somewhat laborious to read.

There are a number of slips and inaccuracies, and the botanical ones have been noticed by previous reviewers. As to animals, one is surprised to find the cole, blue and great tits lumped together as inhabitants of pine and deciduous forest. Admittedly it is stated that the blue and great tits are less common in pine forest, but nowhere is the astonishing abundance of cole tits in this habitat brought out. There is, furthermore, no mention of that characteristic species of northern forests—the bullfinch. In discussing the effects of laying poison for vermin it is said that 'it is impossible to confine its effects to the animals intended to be killed'. This is quite untrue; accidents are due to the use of the wrong poison or to faulty techniques.

However, the book's great merit is to have seen the subject whole and presented it in this way to the reader. Furthermore, even the duller parts are saved by lively writing and by the author's enthusiasm for and appreciation of Scotland and the Scots.

Taking the book as a whole the least satisfactory part (for which presumably the author cannot take much of the blame) lies in the illustrations. The photogravure plates are prone to lose detail in the shadows, and the tones are muddy. The colour plates (reproduced from colour transparencies) are at times reminiscent of the blatant coloured postcards which were popular at the beginning of the century. Yet there are a number of pleasing plates and one (no. 6 of Glencoe) which is very good, so the blame cannot be laid upon the technique of reproduction, but rather on its handling and refinement, wherever, of course, the faults are not in the original transparency. It seems as if one will still have to rely for accurate and consistent colour rendering upon paintings or the more complicated three-colour photographic processes.

H. N. SOUTHERN

TROUT POPULATIONS

D. F. Hobbs (1948). *Trout fisheries in New Zealand: their development and management.* Bull. New Zealand Marine Dep. Fisheries 9: 175 pp.

For generations it has been taken as axiomatic that the hatching and rearing of trout (*Salmo trutta*) under artificial conditions, and the release of the young fish, confers such benefit upon sporting fisheries as fully justifies the expenditure of effort and of funds. In his review of the achievements of hatcheries in New Zealand, Mr Derisley Hobbs points out that this axiom is only true if two conditions be fulfilled. The production of young fish from a female stripped in a hatchery must sensibly exceed the number of young fish which would have been reproduced by that female had she been allowed to spawn in the wild: and the number of young fish turned down from the hatcheries must make a significant contribution to the total population of their species.

Mr Hobbs suggests that up to one-third of the total production of ova by the female fish of a population which is trapped for stripping may be lost as a result of spawning in unsuitable places below the traps. The wastage of ova as a result of imperfect stripping is considered to be about 11 %, as compared with 0·6 % of ova not extruded by wild-spawning fish. Of far greater import is the fact that hatchery operations result in an average production of free-swimming larvae from 67 % of the eggs handled (a figure which may represent the success of not more than 46 % of the total production of ova of the females trapped for stripping), while the average production of natural breeding is the emergence of larvae from 59 to 87 % of the ova.

In dealing with the importance of the contribution of hatcheries to the total population, Mr Hobbs writes of the 'unconscious propaganda of numbers'—the implicit argument of benefit in reports of large-scale releases. It is pointed out that the number of fry released in a year in New Zealand amounts to about 1300 per angler, and that this is equal to no more than the production in the wild of a pair of fish of 2–3 lb. each, and that even this contribution is only a gain to a population in a fishery district where the eggs are brought in from elsewhere. Save in a few peculiar areas, where natural spawning is impossible, hatchery operations are shown to be of little importance or value.

It is suggested that the resources of fishery societies, now devoted largely to hatchery operations, might with advantage be devoted to the protection of spawning fish, the 'salvage' of stocks from drought-stricken areas, the control of enemies and competitors (of which the long-finned eel, *Anguilla dieffenbachii*, seems to be the most formidable) and the safeguarding of environmental conditions.

This report should do much to alter fisheries policies which rest upon no more than respected traditions, not only in New Zealand, but in many other countries.

P. H. T. HARTLEY

THE BADGER IN BRITAIN

Ernest Neal (1948). *The badger.* 158 pp., 12 text-figures, 29 plain and 1 coloured photos. The New Naturalist Monographs, Collins, 14 St James's Place, London. Price 12*s.* 6*d.*

The first of the New Naturalist Monograph series deals with the badger (*Meles meles*), an animal whose ecology has hitherto been little studied: what information there is is scattered in numerous journals and papers which are virtually inaccessible to the ordinary naturalist without considerable expenditure of time and labour. For such people this book provides a convenient summary of the literature and in addition it includes the results of 341 hours spent watching these animals since 1943. The past and present distribution of the badger in Great Britain is given in some detail. Typically it is an animal of wooded hills and appears to be most abundant in the south-west of England and Ireland and virtually absent from the flat areas of East Anglia. It is interesting to find that the Menai Bridge has enabled a pair to establish themselves in Anglesey.

There is very little objective evidence on density in most parts of the country so that different accounts are not strictly comparable; on the whole the tendency is probably to underestimate its density. The number of badgers in Great Britain has markedly increased in the last 25 years; but their distribution and density is still largely determined by the intensity of killing by man. Detailed observations in a Cotswold wood of 45 acres showed that an area this size will support up to three pairs of badgers; an area of 18 square miles in Somerset has a population density estimated at three to the square mile, where the number of cubs reared is thought to balance the numbers of adults lost through trapping.

The badger is an omnivorous feeder, but the relative importance of the various items of its diet is still a matter for speculation. A few stomach contents have been examined and a table is given showing the results of faecal analysis throughout the year. The numbers examined in any one month are small but they do show seasonal trends in the importance of certain items; but as much of the food is soft and easily digested there is little identifiable in many faeces.

The most valuable parts of this book are those dealing with the writer's own observations in the field. Mating is shown to take place in July, the animals probably remaining paired throughout life. The young are born in February, this long gestation period being due, as in some other mustelids, to a delayed implantation of the blastocysts which occurs about January. The young appear above ground in April and remain with their parents until the following autumn. Badgers are social animals and two families will often live together for a time and in the late summer all the animals from neighbouring sets collect at one place; a remarkable photograph is given showing five adults leaving one set. They are said to hibernate, but in the south of England badgers were found to be active in the middle of winter when the temperature was −2° F.

The book is well illustrated, almost over-illustrated, with 30 photographs, some of which are redundant and must increase the cost, which seems high for so small a book; on the other hand, there are one or two photographs mentioned as having been taken by the writer which it would have been interesting to have seen. In order to exercise the reviewer's prerogative of quibbling at minor errors we would point out that the animal whose skins covered the tabernacle of the ancient Israelites and provided them with shoes was the Red Sea dugong and not the badger. This book adds appreciably to our knowledge of the social life and habits of the badger; it is not a critical analysis of the badger's ecology, for which, however, the data available are still inadequate.

J. S. WATSON

BIRD TERRITORY

Eliot Howard (1948). *Territory in bird life.* 224 pp., 11 black and white illustrations, 2 diagrams. Collins, 14 St James's Place, London. Price 10*s.* 6*d.*

Ornithological books and journals are full of studies on territorial behaviour and of discussions on the survival value of territory. The youngest student of birds quickly becomes familiar with procedures, such as mapping bird territories and making observations on the aggressive uses of song and display to obtain and maintain a territory. Before long he is prepared to advance arguments for or against the hypothesis that territory ensures an adequate supply of food for the rearing of a brood.

So much is taken for granted now that it is not easy to visualize the concentrated and painstaking piecing together of evidence that originally built up the territory theory. For half a dozen ornithologists who refer to Eliot Howard's work, there is probably only one who consults his original publications, and this has not been entirely the fault of the student. The first work in which Howard enunciated his conception of bird territory—*The British Warblers*, published in 1907–14—was expensive, appeared in parts and soon went out of print. His later works, including the present one, which was first published in 1920, are not quite so difficult or prohibitive in price to possess, but suffer from the same rarity. It is, therefore, a great boon to students to have available the present edition of a work, in which Howard's main contribution to behaviour theory is embraced; its price is reasonable and its format is perhaps even more satisfactory in some ways than that of the first edition; finally, the original plates have been retained. The publishers are to be congratulated on a very worth-while venture.

H. N. SOUTHERN

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by pointing out omissions and sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, Department of Zoological Field Studies, 91 Banbury Road, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W. 1, or through a bookseller, price 3*s.* 6*d.* per annum post free (in two sets, May and November). Back numbers are available at half price.

Selection and abstracting has been done voluntarily by H. F. Barnes, C. Elton, A. Macfadyen, C. Matheson, E. Nelmes and H. N. Southern; checking by B. M. Hobby.

Within each section the groups are arranged in alphabetical order. Papers dealing with technical methods are dealt with in the appropriate sections.

CONTENTS

	PAGE
1. Ecological surveys and the relations of animals to habitat conditions	128
(*a*) Marine and brackish	128
(*b*) Fresh water	129
(*c*) Land	130
(*d*) Small islands	132
2. General reports and taxonomic studies of use to ecologists	132
3. Parasites	132
4. Food and food habits	133
5. Population studies	134
6. Migration, dispersal and introductions	135
7. Reports of organizations	136

1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and Brackish

Burton, M. (1948). 'Ecology of sponges.' Nature, Lond. 162: 73–4.

Refutes five popular fallacies that (1) sponges grow almost up to high-tide mark, (2) they can survive considerable desiccation, (3) have no enemies, (4) *Hymeniacidon panicea* is the sponge most commonly found on the shore, (5) there is no clear zoning.

Cooper, L. H. N. & Steven, G. A. (1948). 'Marine fish cultivation.' Nature, Lond. 162: 378.

The fertilization of the sea by urban sewage is cited as an example of the poor return to be expected from attempts to increase productivity through adding nutrients.

Das, S. M. (1948). 'British Folliculinidae (Ciliata, Heterotricha).' Nature, Lond. 162: 534.

Folliculinopsis andrewsi, a common species at Wood's Hole, Massachusetts, has been found for the first time on the east side of the Atlantic. Other records of species of Folliculinidae are asked for.

Edwards, G., Hosking, E. & Smith, S. (1948). 'Aggressive display of the oyster-catcher. (Studied by means of stuffed specimens and a mirror).' Brit. Birds, 41: 236–43.

A study, illustrated by many excellent photographs, of the reactions of a pair of nesting oyster-catchers *Haematopus ostralegus* to a stuffed bird and to a mirror. The hen always called up the cock and various forms of aggressive behaviour are described; attacks were severe and always made by the hen. Reactions to a stuffed stoat took quite a different form.

Evans, R. G. (1947). 'Studies on the biology of British limpets.' Proc. Zool. Soc. Lond. 117: 411–23.

The three species of British limpets show distinct differences in vertical distribution with slight overlap. *Patella depressa* has a more southerly range, *P. vulgata* is the most widespread and lives higher up the beach than *P. athletica*.

Gross, F. (1948). 'Marine Fish cultivation.' Nature, Lond. 162: 378.

Advocates further study of the economics of adding fertilizers to the sea.

Hart, T. J. (1948). 'The distribution and biology of hake.' Biol. Rev. 23: 62–80.

The world distribution of the seven species of *Merluccius* is related to that of the main marine currents and coincides mainly with the areas of cold currents flowing towards the equator.

Marshall, N. B. (1948). 'Continuous plankton records: zooplankton (other than Copepoda and young fish) in the North Sea, 1938–39.' Hull Bull. Mar. Ecol. 2, No. 13: 173–213.

Analysis of a large number of plankton counts directed towards a description of plankton regions and their relation to different types of water. Four types are distinguished (1) a north-western one characterized by the chaetognathan *Sagitta elegans*, the euphausiacean *Thysanöessa inermis* and the pteropod *Clione limacina*; (2) a north-eastern one with the euphausiaceans *Meganyctiphanes norvegica* and *Thysanöessa raschii*; (3) a central one with *Sagitta setosa* and a gammarid crustacean *Apherusa clevei*; (4) and a southern one with the caprellid crustacean *Phthisica acaudata*. There is, on the whole, a correspondence with similar indicator groups among the copepods. The distribution of echinoderm and lamellibranch larvae in relation to what is known of adult occurrence is also discussed.

Lucas, C. E. & Stubbings, H. G. (1948). 'Continuous plankton records: size variations in diatoms and their ecological significance.' Hull Bull. Mar. Ecol. 2, No. 12: 133–71.

Analysis of a large number of phytoplankton counts, suggesting that both in *Rhizosolenia styliformis* and *Biddulphia sinensis* the cell size is related to salinity, in zones corresponding with some zooplankton indicators.

Williamson, D. I. (1948). 'Occurrence of *Talorchestia brito* on the coast of Northumberland.' Nature, Lond. 162: 295.

This amphipod has been found locally near Blyth, about 300 miles north of any other recorded point of occurrence.

(*b*) Fresh water

Boyd, H. J. & Alley, R. (1948). 'The function of the head-coloration of the nestling coot and other nestling Rallidae.' Ibis, 90: 582–93.

After discussion of field observations on the coot, *Fulica atra*, it is suggested that the bright head colours of the chicks serve in emphasizing signal movements to elicit feeding by the parents.

Brown, F. Balfour- (1948). 'Re-discovery of *Apus cancriformis*. Nature, Lond. 162: 116.

Despite frequent searches in the locality where *Apus* was found in 1907, no further specimens were found until 1948.

Fox, H. Munro (1948). '*Apus* and a rare cladoceran in Britain.' Nature, Lond. 162: 116.

The primitive crustacean known as *Apus* or *Triops cancriformis* appears to be a permanent inhabitant of Britain. Other records of this species and of *Daphnia ambigua* are asked for.

Hickin, N. E. (1948). 'Larvae of the British Trichoptera—25.' Proc. R. Ent. Soc. Lond. A, 23, 54–6.

Limnophilus rhombicus (Limnophilidae).

Hickin, N. E. (1948). 'Larvae of the British Trichoptera—26.' Proc. R. Ent. Soc. Lond. A, 23: 59–61.

Chaetopteryx villosa (Limnophilidae).

Lichtenstein, E. P. (1948). 'Growth of *Culex molestus* under sterile conditions.' Nature, Lond. 162: 227 (also 999–1000).

Four different media have been found suitable for rearing sterile cultures. Only two other species of mosquitoes have been so reared from egg to adult.

Popham, E. J. (1948). 'Experimental studies of the biological significance of non-cryptic pigmentation with special reference to insects.' Proc. Zool. Soc. Lond. 117: 768–83.

Earlier experiments are extended to minnows and toads as predators and a variety of insects as prey. Use is made of artificial paint marks. In experiments insects harmonizing with their backgrounds are least often destroyed, those which do not harmonize are taken. Toads learned to avoid unpleasant conspicuous forms and *Aeshna* to reject red Hydracarina; and observations on birds showed their ability to catch Hymenoptera without being stung.

Reynoldson, T. B. (1948). 'British species of *Polycelis* (Platyhelminthes).' Nature, Lond. 162: 620–1.

The well-known *Polycelis nigra* has probably been confused with *P. tenuis* on occasions. *P. tenuis* is mottled, is far more heavily preyed upon by the ciliate *Urceolaria mitra*, and prefers stiller waters.

Walshe, B. M. (1948). 'The oxygen requirements and thermal resistance of chironomid larvae from flowing and still waters.' J. Exp. Biol. 25: 35–44.

Measurements of oxygen consumption of closely related species show that those from streams consume more oxygen than those from still water. In the former consumption falls off rapidly with reduced oxygen consumption, in the latter, which are much more resistant to anaerobic conditions, consumption remains constant to a low level of concentration. Thermal resistance of stream forms is also much lower. These findings conform to field measurements of oxygen levels and temperature.

(*c*) Land

Barnes, H. F. (1948). 'Gall midges of economic importance. Vol. iv. Gall midges of ornamental plants and shrubs.' 165 pp. 2 text-figures and 10 photo-plates. Crosby Lockwood and Son Ltd., 20 Tudor Street, London, E.C. 4. Price 15*s*.

This volume, the fourth in a series intended to include eight altogether, is well up to the standard of previous ones, in describing the galls, their distribution in the world, and much about the ecology of the flies, though there are no taxonomic keys to the flies themselves.

Breese, M. H. (1948). 'Notes on the oviposition site and method of reproduction of the weevil *Strophosomus melanogrammus* (Forster) (Col.).' Proc. R. Ent. Soc. Lond. A, 23: 62–5.

Broadbent, L., Doncaster, J. P., Hull, R. & Watson, M. A. (1948). 'Equipment used for trapping and identifying alate aphides.' Proc. R. Ent. Soc. Lond. A, 23: 57–8.

A detachable trap cover of transparent plastic coated with grease-banding substance, removal of the insects, and their preservation and mounting.

Cameron, A. E. (1947). 'Insect and other pests of 1946.' Trans. Highland Agric. Soc. Scot. 59: 65–88.

Includes summary of some results of a team research on Scottish blood-sucking midges of the genus *Culicoides*. Forty-one collections in the Trossachs area containing 6000 specimens, were 96% *C. impunctatus*, which is a serious attacker of man. The remainder were mainly *C. pallidicornis* and *obsoletus*, the last-named being chiefly an urban species. An effective trap was designed for studying species composition in different habitats: it also caught many other insects, and spiders. The habitats of several species were ascertained, but not that of *impunctatus*. Some limited counts of midge larvae in soils indicated average densities of the scale of 9 million per acre. Control measures are discussed.

Cameron, A. E. (1948). 'Insect pests of 1947.' Trans. Highland Agric. Soc. Scot. 60: 58–79.

Includes report on further field trapping research on *Culicoides* spp. to ascertain breeding habitats. Experiments on control.

Clark, E. J. (1948). 'Studies in the ecology of British grasshoppers.' Trans. R. Ent. Soc. Lond. 99: 173–222.

Posthumous notes containing original ideas and suggestions, mainly about the definition and vegetation composition of habitats.

Coombes, R. A. H. (1948). 'The flocking of the raven.' Brit. Birds, 41: 290–4, supplementary note, p. 386.

Observations on flocking habits of this species *Corvus corax* on the west side of Britain (where few, if any, winter immigrants penetrate) suggest that such flocks are mainly composed of sub-adult and non-breeding birds, though mated pairs of adults may join them temporarily.

Davies, L. (1947). 'Observations on the development of *Lucilia sericata* (Mg.) eggs in sheep fleeces.' J. Exp. Biol. 25: 86–102.

Measurements of relative humidity in sheep fleeces by cobalt chloride papers showed that the method is reliable for this purpose. Great variations occur between sheep and with time of day, but humidity is usually too low for the development of the eggs. Occasional higher humidity conditions, especially connected with sweating, were detected; development is possible when 50% R.H. is exceeded at 37°.

Evans, A. C. (1948). 'Studies on the relationships between earthworms and soil fertility. II. Some effects of earthworms on soil structure.' Ann. Appl. Biol. 35: 1–13.

The numbers and size of *Allolobophora longa* and *A. nocturna* determine the weight of wormcasts on the surface of eight agricultural fields. This varies from 1 to 25 tons per acre per annum. Between 4 and 36 tons of soil per acre per annum pass through the total worm population. Wormcasting species of earthworms are associated with a high percentage pore space of soil.

Gunton, H. C. (1948). 'Report on the phenological observations in the British Isles from October, 1946 to September, 1947.' Quart. J. R. Met. Soc. Suppl. to Vol. 74: PR 1–Pr 31. (Published separately, Royal Meteorological Society, 49 Cromwell Road, London, S.W. 7. Price 3*s*.)

This report follows the lines of previous ones in giving the dates of selected biological events (emergence of Lepidoptera, spring flowers, bird song, etc.) recorded by a network of voluntary observers. The results are presented in a concise though indigestible form, mainly as indications of earliness or lateness of various events in relation to weather and to previous years.

Jary, S. G. & Carpenter, K. (1948). 'Insect pests of *Brassica* seed crops in Romney Marsh, Kent.' Ann. Appl. Biol. 35: 134–6.

Field notes on incidence of the blossom beetle (*Meligethes aeneus*), swede seed weevil (*Ceuthorrhynchus assimilis*) and the bladder-pod midge (*Dasyneura brassicae*).

Ross, D. M., Stapley, J. H. & Cockbill, G. F. (1948). 'Wireworm populations in relation to crop production. V. Comparisons between failing and successful crops.' Ann. Appl. Biol. 35: 193–206.

$CaCO_3$ was consistently higher and sand content was consistently lower on the failing plots, those with the higher wireworm population.

Singh, B. N. (1948). 'Studies on giant amoeboid organisms. 1. The distribution of *Leptomyxa reticulata* Goodey in soils of Great Britain and the effect of bacterial food on growth and cyst formation.' J. Gen. Microbiol. 2: 8–14.

Isolation on non-nutrient agar bearing suitable bacteria reveals a previously unsuspected wide distribution. Ninety-two strains of bacteria vary greatly in edibility. The process of and factors influencing cyst formation are considered.

Smith, G. S. (1944–8). 'A season's collecting with a lamp and net.' Rep. Lancs. Chesh Ent. Soc. 68–71: 54–6.

Many moths were collected by means of a 1000 W. lamp run from a generator attached to a 30 h.p. Ford brake van, e.g. on 14–20 April, at Aviemore, 530 specimens of 19 species were taken in this way.

Williams, C. B. (1948). 'The Rothamsted light trap.' Proc. R. Ent. Soc. Lond. A, 23: 80–5.

Description of the trap and various modifications.

(*d*) Small islands

Goddard, T. Russell (1948). 'The Farne Islands: Ornithological Report for 1948.' 7 pp.

A brief summary of the status of bird colonies on this nature reserve of the National Trust.

Lundy Field Society (1948). Second Annual Report. 50 pp.

Miscellaneous ecological notes and lists, mainly about birds, and including some sample counts of nesting seabirds.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Collin, J. E. (1948). 'A short synopsis of the British Sapromyzidae.' Trans. R. Ent. Soc. Lond. 99: 225–42.

Generic and specific keys.

Morison, G. D. (1947). 'Thysanoptera of the London area. (London thrips.). Part I.' Lond. Nat. for 1946, Suppl. 36 pp.

This part of a paper dealing chiefly with the thrips known or likely to occur in the London area includes notes on the anatomy, physiology and bionomics of thrips and on methods of collecting, examining and rearing them, and a key to the adults of the British families.

Norman, J. R. & Fraser, F. C. (1948). 'Giant fishes, whales and dolphins.' Small 8vo, 375 pages; 97 black and white and 7 coloured illustrations by W. P. C. Tenison. Putnam and Co. Ltd., 42 Great Russell Street, London, W.C. 1. Price 15*s*.

This revised edition of a book originally published in 1937 covers the whole world, but will be useful for identifying a number of species, especially of whales and dolphins found in British waters and the Atlantic generally. The text gives concise and authoritative information about the different forms, and the compactness of the book is designed to make it convenient for sea travellers.

3. PARASITES

Arthur, D. R. (1948). 'Some aspects of the ecology of the tick, *Ixodes ricinus*, L., in Wales.' Bull. Ent. Res. 39: 321–37.

The distribution of ticks is influenced by superficial soil deposits; the vegetation index of tick infested land is variable. Greater populations and a greater rate of activity were apparent in rush land than on bracken, heather-winberry and lay land. A salt marsh adjoining an infested non-salt marsh was free of ticks. 'Islands' of damp ground harbour ticks.

Cockings, K. L. (1948). 'Successful methods of trapping *Trombicula* (Acarina) with notes on rearing *T. deliensis*, Walch.' Bull. Ent. Res. 39: 281–96.

Live unfed larvae in the field may be concentrated and trapped by the use of a low cover with a central light-admitting aperture and collecting apparatus. Guinea-pigs can be used as bait animals for the collection of *Trombicula autumnalis*. Engorged larvae may be easily collected as they leave their host (or dead animals and debris) by the funicular laboratory light-trap which is described. The method of collecting adult mites and nymphs from soil flotation in water is discussed.

Dales, R. P. (1948). 'Occurrence of *Acanthocephalus ranae* Schrank. in Great Britain.' Nature, Lond. 162: 1001.

Third British record of the only known Acanthocephalan parasite of the frog.

Milne, A. (1948). 'Pasture improvement and the control of sheep tick (*Ixodes ricinus* L.).' Ann. Appl. Biol. 35: 369–78.

The improvement of rough poor hill and moorland pastures involves a reduction in the depth of the vegetation layer and partial or complete reduction in the underlying mat of decaying vegetable matter. The tick population also decreases probably on account of the reduction in cover and so humidity.

Reynoldson, T. B. (1947). 'Urceolarian epizoites of flatworms.' Nature, Lond. 160: 265–6.

The ciliate *Urecolaria mitra* was found not to attack the flatworm *Dugesia lugubris* but to occur in large numbers on *Polycelis nigra*. There was an inverse correlation between numbers of ciliates and size of flatworm.

Simmonds, F. J. (1948). 'Some difficulties in determining by means of field samples the true value of parasite control.' Bull. Ent. Res. 39: 435–40.

Certain difficulties of a biological nature inherent in the estimation of the degree of control exerted by individual parasite species.

4. FOOD AND FOOD HABITS

Evans, A. C. (1948). 'The identity of earthworms stored by moles.' Proc. Zool. Soc. Lond. 118: 356–9.

Stores of earthworms made by moles (usually containing some 30–60 specimens) include disproportionately high numbers of *Lumbricus terrestris* and very few *L. castaneus* and *Allolobophora chlorotica* when compared with the available fauna in the soil, where *L. terrestris* is less common than *A. caliginosa* and *A. longa*. From the little harm done to the worms it is suspected that they have been caught in the runs and not pulled out of the soil while burrowing.

Hartley, P. H. T. (1948). 'The assessment of the food of birds.' Ibis, 90: 361–81.

A general critique of methods used to estimate the food of birds. Few adequate quantitative studies of any species have been made, and material is seldom collected against a satisfactory background of field study. Furthermore, the various numerical and volumetric methods of expressing results of stomach and crop analyses need to be adapted carefully to each species studied. Pronouncements on 'economic status' have rarely any value.

Kay, G. T. (1948). 'The gannet in Shetland in winter.' Brit. Birds, 41: 268–70.

Unusually large numbers of gannets, *Sula bassana*, occurred in Shetland during the winter of 1945–6, feeding on an abundance of coal-fish, *Gadus virens*. Since the establishment of the gannet as a Shetland breeding species (1914) there have been many winters with large shoals of coal-fish, but in this case they were unusually large and it is suggested that the gannet prefers to feed on prey about 1 ft. in length.

Owen, J. H. (1948). 'The larder of the red-backed shrike.' Brit. Birds, 41: 200–3.

Contains qualitative notes on larder contents of this species *Lanius collurio* and general comments on the habit. Larders are frequently filled up in the evening and emptied in the early morning.

Ribbands, C. R. (1948). 'The foraging behaviour of honey bees.' Agriculture, 55: 252–5.

Popular account of von Frisch's experiments, in connexion with the pollination of red clover.

Thompson, H. V. (1948). 'Studies of the behaviour of the common brown rat (*Rattus norvegicus*, Berkenhout). I. Watching marked rats taking plain and poison bait.' Bull. Anim. Behav. No. 6: 26–40.

Population size was estimated from the changes in consumption of prebait after the removal of thirteen rats and again when they were returned after marking. The marks enabled observers to record the feeding behaviour of individuals attracted to feed in a lighted shed. On successive nights the rats fed more and more eagerly.

5. POPULATION STUDIES

Allen, P., Brambell, F. W. R. & Mills, I. H. (1947). 'Studies on sterility and prenatal mortality in wild rabbits. I. The reliability of estimates of prenatal mortality based on counts of corpora lutea, implantation sites and embryos.' J. Exp. Biol. 23: 312–45.

The gelatinous yolk-sac contents of embryos in wild rabbits, which condition is related to prenatal mortality, are shown to be due to a fibrin clot and not a pathogenic organism.

Corbin, P. G. (1947). 'The spawning of mackerel, *Scomber scombrus* L., and pilchard, *Clupea pilchardus* Walbaum, in the Celtic Sea in 1937–39 with observations on the zooplankton indicator species, *Sagitta* and *Muggiaea*.' J. Mar. Biol. Ass. U.K. 27: 65–132.

Mackerel spawned from mid-March to the end of July, pilchards from April to July. Very extensive data on distribution.

Corbin, P. G. (1948). 'On the seasonal abundance of young fish. IX. The year 1947.' J. Mar. Biol. Ass. U.K. 27: 718–22.

There has been little improvement in catch since 1939 which was the worst year recorded.

Das, S. M. & Seshappa, G. (1948). 'A contribution to the biology of *Patella*: on population distribution and sex-proportions in *Patella vulgata* Linnaeus at Cullercoats, England.' Proc. Zool. Soc. Lond. 117: 653–62.

The vertical distribution of *Patella vulgata* is described. Maximum size of individuals occurs at the highest levels whilst largest numbers are found lower on the beach. The sex ratio varies with degree of exposure.

Fitter, R. S. R. (1948). 'Report of the black redstart inquiry for 1947.' Brit. Birds, 41: 267.

At least 15 pairs of this newly acquired British species (*Phoenicurus ochrurus*) bred in 1947.

Guild, W. J. McL. (1948). 'Studies on the relationship between earthworms and soil fertility. III. The effect of soil type on the structure of earthworm populations.' Ann. Appl. Biol. 35: 181–92.

The total population numbers and relative numbers of each species vary according to the soil type. In the Carse of Stirling *Allolobophora caliginosa* is the dominant species, *A. longa* is subdominant and forms a substantial percentage on medium loam and clay, but is of reduced importance (percentage of total population) on light loam, gravelly sand and alluvium where it does not differ much from *Lumbricus rubellus* and *L. terrestris*. The *Lumbricus* population number is highest on light loam and lowest on clay. Areas of acid natural pastures contain earthworm populations low in number and species variety. Such areas contain *Dendrobaena rubida, D. octaedra* and *Bimastus eiseni* which are not found in well-established fields.

Höhn, E. O. (1948). 'Mortality of adult and young mallards.' Brit. Birds, 41: 233–5.

Ringing recoveries for over 1000 mallard, *Anas platyrhyncha*, show that the mean expectation of life for those ringed as young is 4·5 months, but of those ringed as adults it is 1 year and 2 months.

Keighley, J. & Buxton, E. J. M. (1948). 'The incubation period of the oyster-catcher.' Brit. Birds, 41: 261–6.

Detailed notes on the incubation of this species, *Haematopus ostralegus*, made at Skokholm, Pembrokeshire. The usual period varies between 25 and 29 days, the longer periods being usually at nests which are much disturbed. The order of laying is not necessarily correlated with the order of hatching.

Lucas, C. E. (1947). 'The biological effects of external metabolites.' Biol. Rev. 22: 270–95.

From a consideration of the importance of antibiotics in the ecology of micro-organisms this paper passes to the evidence for similar relationships—involving both harmful and beneficial effects—among higher organisms. It is suggested that 'animal exclusion' by phytoplankton, sex determination by excretions and effects of root products can be profitably considered in this light, and that development of favourable responses to such products has been an important factor in the evolution of species and of communities.

Parrinder, E. R. (1948). 'The little ringed plover in southern England in 1948.' Brit. Birds, 41: 377–83.

Chislett, R., Dawson, K. & Allison, K. R. (1948). 'The little ringed plover in Yorkshire.' Brit. Birds, 41: 384–5.

This species *Charadrius dubius*, which only established itself as a breeding species in Britain in 1944, increased in numbers in the counties round London and extended its breeding range to Yorkshire in 1948.

Richards, O. W. (1948). 'The interaction of environmental and genetic factors in determining the weight of grain weevils, *Calandra granaria* (L.) (Col., Curculionidae).' Proc. Zool. Soc. Lond. 118: 49–81.

Size of weevils varies with depth of medium and population density, this being attributed to accumulation of metabolic products. Size of grains, time of emergence in relation to the remainder of a batch and heredity are also important.

Stuart, D. (1948). 'Vital statistics of the Mochrum cormorant colony.' Brit. Birds, 41: 194–9, 389.

An analysis of 172 ringing recoveries between 1919 and 1939 of cormorants, *Phalacrocorax carbo*, at a colony in Wigtownshire shows a high juvenile mortality during the first 6 months of life. The figures give a mortality rate of 70% in the first year of life and of 25–43% in subsequent years, but since this is too great to maintain the breeding stock at its observed level with the observed rate of productivity, it is probable that there are sources of error in the data, e.g. loss of rings. Maps are given of the distribution of recoveries and show a dispersal predominantly southward.

Thomas, I. (1948). 'Insect damage assessment.' Agriculture, 55: 125–9.

Scheme of the Conference of Advisory Entomologists to record fluctuations from year to year in insect populations and in damage done, to determine the extent to which the overwintering egg populations of certain insects are related to subsequent infestations on summer hosts and ultimately perhaps to forecast outbreaks. Notes on frit fly, cabbage aphis and black bean aphis.

Ticehurst, N. F. & Hartley, P. H. T. (1948). 'Report on the effect of the severe winter of 1946–1947 on bird-life.' Brit. Birds, 41: 322–34.

Reports collected from all parts of the country show that species were differently affected in different places. Many weather movements were observed, especially along the Sussex coast, and many local 'exterminations' of such species as woodlark, titmice (including bearded tit), stonechat, kingfisher, wren, etc. are recorded.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Broadbent, L. (1948). 'Aphis migration and the efficiency of the trapping method.' Ann. Appl. Biol. 35: 379–94.

Different species fly at different heights. The number of aphides caught was roughly proportional to the volume of free air space round the traps (adhesive). Conditions for voluntary aphis flight in and near the crop are often suitable on relatively windy days. Voluntary flight decreased with increasing height. Brilliant yellow traps coated with adhesive grease, caught more aphides than white traps, which caught more than black ones.

Gislén, T. (1948). 'Aerial plankton and its conditions of life.' Biol. Rev. 23: 109–26.

Considers the biological and size characteristics of the animals found in the aerial plankton and especially their resistance to temperature, pressure and drought. The smallest forms are mostly highly specialized but extremely efficiently distributed and capable of rapid multiplication when a suitable habitat is encountered. This is aided by asexual methods of reproduction.

Pinniger, E. B. (1947). '*Coenagrion scitulum* Rambur, a dragonfly new to Britain.' Lond. Nat. for 1946, 26: 80.

A male and two females were captured in south-east Essex in July 1946.

7. REPORTS OF ORGANIZATIONS

Bedfordshire Natural History Society & Field Club (1947–8).

This Society, which had a brief existence at the end of the nineteenth century, has recently been re-started, and now produces 'The Bedfordshire Naturalist' (No. 2, for 1947, 1948; the first number having been called the 'Journal' of the Society). It contains numerous lists and ecological notes of local and some of general interest.

Freshwater Biological Association of the British Empire (1948). Sixteenth Annual Report for the year ending 31st March, 1948. 50 pp. (Price to Non-members, 1*s.* 6*d.* F.B.A., Wray Castle, Ambleside, Westmorland.)

Review of current work and list of recent publications.

London Natural History Society (1947). 'The Survey of Bookham Common. Fifth Year.' Lond. Nat. for 1946, 26: 81–93.

The work undertaken during 1946 and outlined by C. P. Castell (pp. 81–2) included the collection of fresh-water and land molluscs and of Diptera, a study of aquatic beetle populations in gun-pits and bomb craters and their seasonal changes, and another of the density in spring of robins, blackbirds and chaffinches; 25 robin song-posts were mapped, and the density of the territories was found to vary from 2·7 to 10 per 10 acres. The report includes an annotated list, by A. M. Easton (pp. 87–93), of 36 species of Malacodermata and 95 of Phytophaga, mostly taken during the past ten years, by beating or sweeping, with additions made in 1946 to a similar list of Rhynchophora [Lond. Nat. No. 25 (1946)], as well as two maps of the woodland vegetation and a preliminary list of fungi.

London Natural History Society (1947). 'The Epping Forest Survey. Fifth Year.' Lond. Nat. for 1946, 26: 94–117.

J. Ross (pp. 94–9) gives a list of Cynipid wasps and galls found on oak over a period of years and compares their present abundance with that indicated in a list drawn up in 1901. D. W. Vere (pp. 99–109) describes observations on the distribution, habits and behaviour of hornets (*Vespa crabro*) in 1945, which established that they occur quite commonly round the margin of Epping Forest, though rarely more than 100 yards from the edge, and that in the main observation area they were confined to oak wood and avoided an adjoining beech-hornbeam wood in which there were a few oaks. Some trees in the oakwood were infected with a white slime-flux, and this exudation from oaks and hornbeams formed the staple food of the hornets in the early part of the year and appeared to be transmitted by them. D. G. Tucker (pp. 109–16) gives the number of times during winter (December–March) and spring (April–July) that various mammals and birds were recorded in Highams Park in the course of about 50 walks, each over the same route and occupying about 45 min. The results in the case of birds are analysed statistically. The average number of individuals and species observed were both lowest when fewer than 20 people were seen, and these reductions were found to be significant and highly significant, respectively. Weather did not appear to be correlated with bird numbers, but the number of species, but not individuals, seen was significantly greater early in the day than later. Since the human population was small early in the day and the correlation with this factor was most significant, it is regarded as the main one affecting numbers in this wood.

Parrinder, E. R. (ed.) **(1947).** The London Bird Report for 1946. No. 11. 36 pp.

This report includes an annotated list of 130 birds recorded in the London area during 1946, a note on the field identification of glaucous and Iceland gulls (*Larus hyperboreus* and *L. leucopterus*), the results of a rookery survey and a census of great crested grebe (*Podiceps cristatus*), and observations on the breeding of black redstarts (*Phoenicurus ochrurus*). The results of rookery surveys in 1945 and 1946 indicated that the number of rookeries and breeding pairs of rooks (*Corvus frugilegus*) in the area in 1945 probably did not exceed 360 and 10,000, respectively. There are no rookeries within a radius of 6–10 miles from the centre of London; beyond this zone, there are concentric belts in which the number of nests per square mile increases to six, and outside these there are 4–5 areas with populations of over 24 nests per square mile. The number of great crested grebe in the country has decreased by less than 5% since 1931, but in London, numbers increased from 225 to 356; most birds were in Middlesex, where the density (69 birds per 100,000 acres) was almost twice that of any other county. The rise is attributed to the increasing number of gravel pits. There were fewer birds on other waters, and non-breeding birds were almost twice as numerous as breeding ones. In 1935, the total number of adults in the country was about the same as in 1931, but the number in London had decreased by about 10%. Six pairs of black redstart, three of which were known to have nested, were reported within the City of London, but only three non-singing males. For the first time in 21 years, no black redstarts were reported from Outer London during the breeding season.

Shaw, H. K. Airy (1948). 'Directory of Natural History Societies.' Amat. Ent. Soc. Pamph. No. 7: 1–155.

Gives historical details, conditions of membership, frequency of meetings and publications, library and other amenities.